



TAPHONOMIC ANALYSIS AND PALEOBIOLOGICAL OBSERVATIONS OF *CROSSVALLIA UNIENWILLIA* TAMBUSSI ET AL. 2005, THE OLDEST PENGUIN FROM ANTARCTICA

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Abstract. The purpose of this paper is to provide a taphonomic analysis of the holotype of *Crossvallia unienwillia* Tambussi, Reguero, Marenssi and Santillana, 2005, in order to improve the knowledge of the vertebrate record of the Cross Valley Formation, a unit exposed in the central area of Marambio (Seymour) Island, Antarctic Peninsula. Analyses of the preservational state of the skeleton assigned to *Crossvallia unienwillia* offer important data for palaeoenvironmental and depositional reconstructions, key for the understanding of the early evolutionary history of penguins. Different techniques, including petrographic sections, SEM observation, Secondary Electrons Detectors, backscattered electrons detectors, microanalysis for probe of electrons, and X-ray diffraction were applied in order to distinguish biostratinomic from fossil diagenetic damage. Fossil bones of *Crossvallia* are associated with a typical marine assemblage including shark remains and macroinvertebrates. The hosting mudstones suggest a low-energy environment either below the wave-base or protected from wave action. In any case initial marine conditions changed to other with regular influx of land-derived sedimentary material. *Crossvallia unienwillia* was a female diver that passed through several molting periods before death. Biostratinomic processes consistent with little transport and rapid burial which would have prevented the action of destructive processes such as weathering and carnivores or scavenging, are inferred. The rapid burial favored the initial preservation of the elements under anoxic conditions. The surficial corrosion, fractures, and the internal filling of the cavities, suggest that destructive processes were only important after final burial during the telodiagenetic stage. The absence of more vertebrate fossil remains in the Cross Valley C Allomember is the result of those destructive processes, whereas on the contrary the original depositional environment appears to have been optimal.

Key words. Fossil Penguin. Cross Valley. Marambio Island. Paleocene, Antarctic Peninsula.

Resumen. ANÁLISIS TAFONÓMICO DE *CROSSVALLIA UNIENWILLIA* TAMBUSSI ET AL. 2005: EL PINGÜINO MÁS ANTIGUO DE ANTÁRTIDA. El objetivo de este trabajo es el análisis tafonómico del holotipo de *Crossvallia unienwillia* Tambussi, Reguero, Marenssi and Santillana, 2005, con el fin de incrementar el conocimiento acerca del registro fósil de vertebrados de la Formación Cross Valley, aflorante en el área central de la Isla Marambio (Seymour), Península Antártica. El análisis del estado preservacional de los restos de *Crossvallia unienwillia* ofrece importantes datos para las reconstrucciones paleoambientales y áreas depositacionales, claves para la comprensión de la historia evolutiva temprana de los pingüinos. Diferentes técnicas, incluyendo el estudio de secciones petrográficas, observaciones en MEB, detector de electrones secundarios, detector de electrones dispersos, difracción de rayos X y rayos X de energía dispersiva, fueron aplicados para distinguir las alteraciones bioestratinómicas de aquellas fósil-diagenéticas. Los restos de *Crossvallia* forman parte de una asociación típicamente marina, incluyendo además tiburones y macroinvertebrados. Los sedimentos portadores indican un ambiente de baja energía, ya sea por debajo del tren de olas, o bien protegido de la acción de las olas. En cualquiera de estos casos, las condiciones marinas iniciales cambiaron hacia otras con un flujo regular de material continental sedimentario. *Crossvallia unienwillia* fue una hembra buceadora, que atravesó varios periodos de muda antes de su muerte. Procesos bioestratinómicos consistentes con un bajo transporte y un rápido sepultamiento que habría prevenido la acción de procesos destructivos tales como la meteorización son inferidos para este caso. El enterramiento rápido favoreció la preservación de los elementos bajo condiciones anóxicas. La corrosión superficial, las fracturas y el relleno de cavidades internas, sugiere que los procesos destructivos fueron solo importantes luego del sepultamiento durante estadios telodiagenéticos. La ausencia de otros vertebrados fósiles en el Alomiembro Cross Valley C es el resultado de esos procesos, mientras que de manera contraria, el ambiente depositacional pareció haber sido óptimo.

Palabras clave. Pingüino Fósil. Cross Valley. Isla Marambio. Paleoceno. Península Antártica.

THE material for this study comes from the type section of the Late Paleocene Cross Valley Formation (Elliot and Trautman, 1982; Montes *et al.*, 2013) located in the central area of Marambio (Seymour) Island, Antarctic Peninsula. The Cross Valley Formation is bounded by two main unconformities from (1) the underlying Danian Sobral Formation (and probably also from the Maastrichtian–Danian López de Bertodano Formation) and (2) the overlying Eocene La Meseta Formation (Santillana and Marensi, 1997; Montes *et al.*, 2007; Marensi *et al.*, 2012). Dinoflagellates and Strontium-derived ages ($\text{Sr}^{87}/\text{Sr}^{86}$) allowed estimating a Selandian–Thanetian age for this unit (Palamarczuk *et al.*, 1984; Askin, 1988; Wrenn and Hart, 1988; Marensi and Santillana, 2003).

Among the vertebrates recovered from this unit are part of a non-articulated penguin skeleton assigned to *Crossvallia unienwillia* Tambussi, Reguero, Marensi and Santillana, 2005; an isolated penguin diaphysis and some fish bones. The penguin diaphysis (MLP 00-I-1-16) belongs to a Spheniscidae indet. consistent in size with *Crossvallia unienwillia* but poorly preserved. Fish material includes several bone fragments of Teleostei indet. (MLP 00-I-17 and MLP 00-I-18) and shark teeth (MLP 14-I-10-82). The holotype of *Crossvallia unienwillia* is the only skeleton known from this unit (MLP 00-I-10-1); fossils were found associated and are the holotype and only elements known for this species (Tambussi *et al.*, 2005; Jadwiszczak *et al.*, 2013a).

Further paleontological field work in this locality confirmed the scarcity of vertebrates in this unit. By contrast, fossil leaves and other plant remains are common in the upper part of the same level (Dusén, 1908; Cantrill *et al.*, 2011). *Crossvallia* represents an important case, not only for the study of penguins and the Antarctic fauna in general, but also because it helps understanding the taphonomic history of the Cross Valley Formation vertebrates.

Analyses of the preservational state of *Crossvallia unienwillia* offer important data for palaeoenvironmental and depositional reconstructions, and constitute a key for understanding the early evolutionary history of penguins. This knowledge could become extremely useful for planning and prospecting these strata in the near future. In this sense, the purpose of this paper is to provide a taphonomic analysis –biostratigraphic and fossil-diagenetic– of the fossil remains in order to improve the knowledge of the vertebrate fossil record in the Cross Valley Formation.

GEOLOGIC SETTING

The Cross Valley Formation is 195 meters thick and fills in a narrow valley with volcanoclastic deposits representing an incised valley system, including estuarine, shallow marine and deltaic facies (Marensi *et al.*, 2012). Recent field-work allowed subdividing this formation into three unconformity-bounded subunits or allomembers named A to C from base to top (Santillana *et al.*, 2007; Marensi *et al.*, 2012; Montes *et al.*, 2013). A detailed sedimentologic and petrographic description of this unit has been recently published by Marensi *et al.* (2012).

Cross Valley A Allomember. The base of the unit is a 0.30 to 1 meter thick medium-grained massive sandstone bed rich in glauconite. Most of the allomember is composed of coarse- to fine-grained cross-bedded sandstone with a high percentage of volcanic material arranged into three fining-upward cycles 30 to 40 meters thick. Charred wood is frequently included in the sandstone. This allomember is interpreted as deposited in subtidal channels in an incised valley (Montes *et al.*, 2007; Marensi *et al.*, 2012).

Cross Valley B Allomember. The base of this unit is a subtle erosive surface covered by coarse-grained to gravelly sandstones. Three main lithofacies about 35 m thick compose this allomember. A lower interval made up of coarse-grained massive sandstone, a middle part composed of coarse- to medium-grained parallel-laminated sandstone and an upper section made up of inter-bedded medium-grained sandstone and mudstone. Angular to subangular volcanic clasts –including pumice– comprise more than 80% of the sand and gravel fraction. This allomember records submarine volcanoclastic (laharic-type?) sedimentation within an incised valley (Amoedo, 1992; Doktor *et al.*, 1988; Montes *et al.*, 2007; Marensi *et al.*, 2012).

Cross Valley C Allomember. This unit is about 15–20 m thick and covers the former, from which it is separated by an erosive surface locally draped by angular blocks (up to 0.40 m in diameter) of the underlying unit. The lower part is composed of grey calcareous mudstone containing occasional fish and shark teeth, gastropods, echinoids and penguin bones (Tambussi *et al.*, 2005). The upper part is made up of inter-bedded fine-grained parallel-laminated to ripple cross-laminated light sandstone and dark mudstone containing large wood fragments and discrete levels of plant debris (Dusén, 1908; Cantrill *et al.*, 2011). The sandstone

composition changes from base to top. Rock fragments in the sand-sized fraction are dominated by volcanics in the base but plutonic and metamorphic detritus become dominant towards the top. Sandstone is mainly cemented by calcium carbonate (both sparite and micrite) but some diagenetic clays and iron oxides are locally present. This allomember represents sedimentation in shallow marine to marginal deltaic (interdistributary bays) environments (Elliot and Trautman, 1982; Marensi *et al.*, 2012).

The Cross Valley Formation has been interpreted as representing different sedimentary environments within a coastal setting. Elliot *et al.* (1975) interpreted it as deposited in mixed fluvial and deltaic environments, while Elliot and Trautman (1982) restricted their interpretation to a deltaic origin. Later, Sadler (1988) demonstrated that the Cross Valley Formation fills in a narrow submarine valley. Doktor *et al.* (1988) and Amoedo (1992) described deltaic and volcanoclastic lahar-like deposits. Finally, Montes *et al.* (2007) and Marensi *et al.* (2012) interpreted the Cross Valley Formation as an incised valley fill system with a lower subtidal volcanoclastic section (allomembers A and B) and an upper deltaic member (Allomember C).

MATERIALS AND METHODS

Materials under study are housed in the Museo de La Plata (MLP), La Plata, Argentina. The penguin fossil bones (MLP 00-I-10-1 and MLP 00-I-1-16), and the fish remains

(MLP 00-I-17, MLP 00-I-18, and MLP 14-I-10-82) were collected during field work organized by the Instituto Antártico Argentino, in the late Paleocene Cross Valley Formation (lower part of Allomember C) at locality GPS: 64° 15' 50" S; 56° 40' 0" W (Fig. 1.1) (Seymour-Marambio Island), Antarctica (see Tambussi *et al.*, 2005).

Penguin material was described using a stereoscopic microscope Arcano ZTX Zoom (10–40x). Fractures were classified according to their genesis, distinguishing biotratynomic from fossil-diagenetic damage following the classical criteria of Behrensmeier (1978).

Osteological terminology follows Baumel and Witmer (1993). Measurements were taken with a Vernier Caliper accurate to 0.1 mm. The ratio of the marrow area to the whole section of the bone was calculated following Meister (1962).

The petrographic analysis was made on a thin section of long bone prepared by means of the total rock technique. A Zeiss STEMI 2000-C binocular microscope with a CANON power Shot C10 camera was used for obtaining a general image of the CT. Thin sections were analyzed with a Leitz Laborlux 12 Pol petrographic microscope with a Leica DFC290 HD photographic digital camera. Images were captured using the Leica Application Suite V3 version 3.7; pictures were taken with plane-polarizer (pp) and without plane-polarizer (wp).

SEM (Scanning Electron Microscope) observations of the material were using a FEI ESEM Quanta 200 with electron

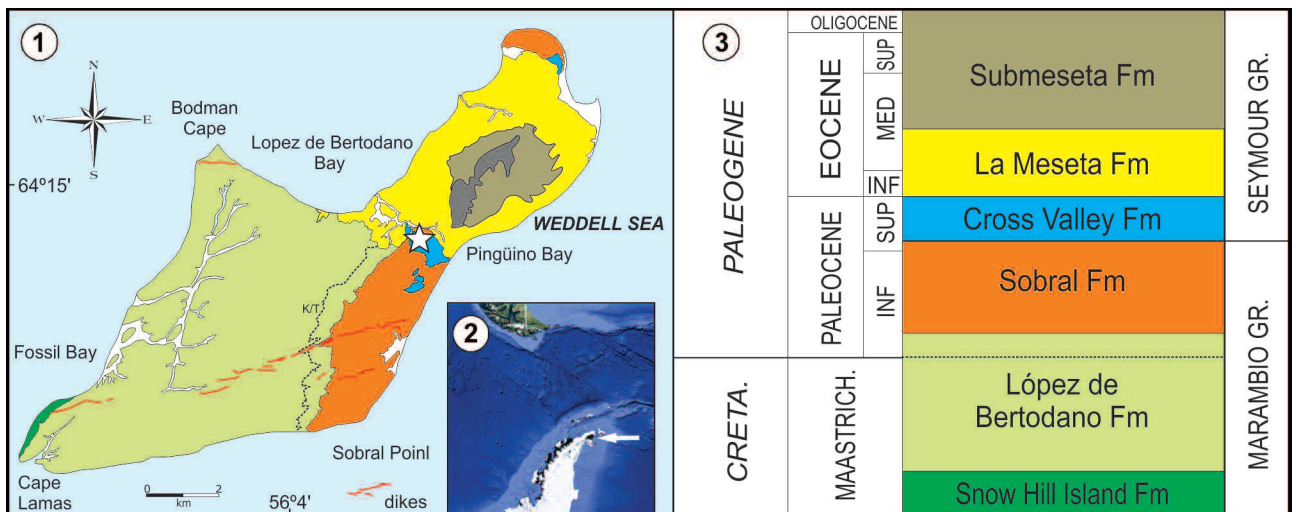


Figure 1. 1, Map of the study area; the star indicates the *Crossvallia* locality; 2, General location of the Marambio (Seymour) Island indicated by the arrow; 3, Stratigraphic scheme showing the relationship of the Cross Valley Formation (modified from Montes *et al.*, 2013).

source from a tungsten filament, with accelerating voltage of 200 V – 30 kV at the Departamento de Mecánica, LIMF service (Facultad de Ingeniería, UNLP). The sample was analyzed in Low Vacuum mode (LoVac) with a precision of 0.1 to 1 Torr, without metalizing. Secondary Electron detectors, were used looking for a high topographic contrast image of the examined surface.

Backscattered electrons (BE) detectors of two sectors BSED were employed in order to observe variations in the atomic number (Z) of the elements detected on surface. Heterogeneity of the sample is expressed in the image through different gray tonalities depending on the atomic number (for a further explanation see Galván Josa *et al.*, 2013).

Microanalysis for probe of electrons (dispersive in energy X-ray Spectrometer) EDAX SDD Apollo 40 was performed. It implies the detection of light elements from boron, resolution <135 eV, with a qualitative, semi-quantitative, and quantitative analysis capacity, and patterns for chemical elements microanalysis in a sample of 1 mm³.

The X-ray diffraction analysis was made on a fine material sifted by a mesh (<20 microns), measured with a PANalytical X'Pert PRO diffractometer with a CU lamp ($k=1.5403 \text{ \AA}$), to 40 m \AA and 40 kV. Samples were measured from 4 to 37°, with a scanning speed of 0.04°/s. The software Origin was selected for the edition of the results. This study and the petrographic analysis were made in the Centro de Investigaciones Geológicas (CIG - CONICET) in La Plata. Sam-



Figure 2. Image of the discovery with the specimen of *Crossvallia unienwillia* lying *in situ*, where the space relationships among the penguin fossil bones are observed.

ples were represented by bony fragments associated to the holotype of *Crossvallia unienwillia*, the Spheniscidae indet. from the late Eocene Submeseta Formation, and the living *Pygoscelis adeliae* (Hombron and Jacquinot, 1841).

Stratigraphy is according to Marensi *et al.* (2012) and Montes *et al.* (2013).

RESULTS

Crossvallia unienwillia (holotype MLP 00-I-10-1) was described on the basis of a partial skeleton (an almost complete left humerus and a right femur, the proximal and distal end of a right tibiotarsus, an incomplete thoracic vertebra and other 28 unidentifiable remains, see Jadwyszczak *et al.*, 2013a), whose elements were found associated on the surface (Fig. 2).

Macroscopic observations

The humerus is complete but preserved in several pieces. The periosteal bone layer and both epiphyses are well preserved, but some signs of chemical alteration are observed, such as the change in the composition of the surficial bone. Quartz grains are accreted at the proximal end, and other siliciclastic sediments are added in patches on the diaphysis. The tridimensional relationships are well preserved with no observable deformation. Signs of surface weathering (according to Behrensmeyer, 1978) or flaking off in the periosteal bone are absent. Neither longitudinal fractures along the main axis nor any fracture with eyelet morphologies are present. On the contrary, perpendicular or oblique fractures are abundant in the diaphysis (Fig. 3.1). The internal cavity is not filled or substituted by sediment, and trabecular tissues are observed.

The femur is badly damaged, and preserved in several pieces. The periosteal bone layer and the epiphyses are highly altered by chemical corrosion (Fig. 3.2). Osteological features at the proximal end are abraded and covered by sulfate deposits. Signs of weathering are mainly observed at the distal end, where the trabecular bone is exposed. By contrast, the diaphyseal periosteal bone remains non-flaked and mineral precipitates fill the inner spaces of the shaft.

The epiphyses of the tibiotarsus (and a little portion of the diaphysis) are completely damaged and present transversal fractures (Fig. 3.3). The same preservational attributes described for the proximal end of the femur (Fig. 3.2) are

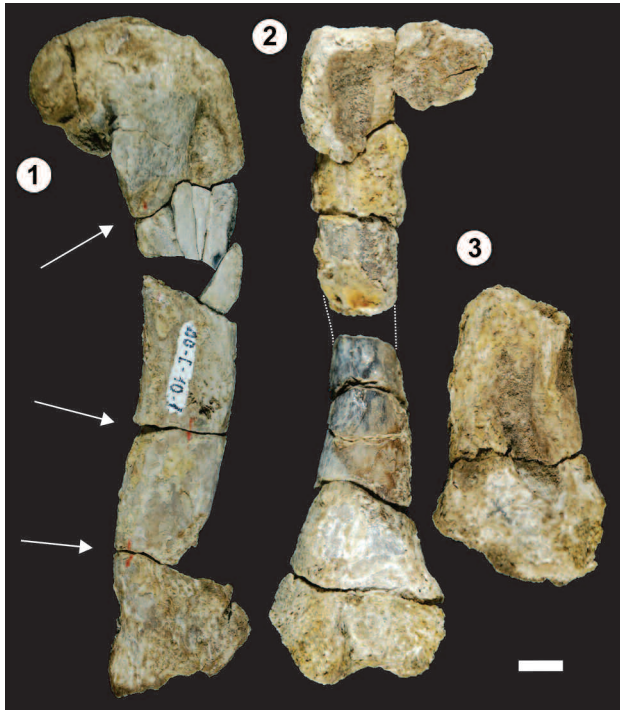


Figure 3. 1, Left humerus with oblique and transverse fractures in cranial view, see the arrows; 2, Right femur in cranial view (see the evidence of chemical corrosion in the proximal epiphysis, and the transverse fractures in the distal end); 3, distal epiphysis of right tibiotarsus with signs of corrosion and mineral deposits. Scale bar= 50 mm.

present here (mineral deposits, corrosion, etc.).

The unidentified fragments associated with the holotype of *Crossvallia* have flat and clean fractures, perpendicular to the bony tissue fibers. The characteristic pachyosteosclerosis developed in all penguin bones is also present here. However, the degree of specialization is lower than that of recent penguins (see discussion below).

In summary, signs of weathering such as longitudinal fractures, flaking and polished surface are not observed in these bones. Traces attributed to trampling by other animals, scavenging or carnivores marks (Cione *et al.*, 2010) were not identified.

Microscopic observations (Petrographic section)

Histology. The histological arrangement of the bone in the specimen of *Crossvallia unienwillia* is similar to that in other birds (Meister, 1951 and shows differences only in the distribution of the bony fabric. The concentric histological structure previously recognized in modern penguins (Meis-

ter, 1962; de Margerie *et al.*, 2004) and also in extinct forms (Yury-Yáñez *et al.*, 2012; Cerda *et al.*, 2015) was observed in the specimen studied (Fig. 4.1). It includes the development of pachyosteosclerosis (Houssaye, 2009) according to the classification of de Ricqlès and de Buffrénil (2001) for bone hypertrophy non- associated to pathological contexts.

A detailed comparison of the proportions of each bony layer in the different penguin species allows the recognition of different levels or degrees of specializations (see below). In *Crossvallia* the periosteal bone is moderate, the compact bone represents the main part of the volume, and the trabecular bone constitutes an intermediate-volume layer contacting and invading the marrow cavity (Fig. 4.2). The relationship between the medullar cavity and wall thickness is 1: 2.03 in the specimen of *Crossvallia unienwillia* (see Meister, 1962), meaning that the medullar area occupies about 49% of the area in section.

The periosteal bone layer is the dark brownish layer composed by an outer dense fibrolamellar tissue with few vestigial vascular spaces and canaliculi (Fig. 4.3). It constitutes 8% of the ratio in transversal section.

Toward the inner part, two compact bone areas equal in size amount to 51% of the ratio. The most external one is compact and less vascularized, with a denser bioapatite matrix. The inner one is characterized by more vascularized tissue (Fig. 4.2, 4.5). Abundant and well defined primary osteons with Haversian system surrounded by lamellae and canaliculi are homogeneously distributed. They constitute large resorption-originated cavities that sometimes are partially filled by carbonate with centrifugal growing and other amorphous compounds (Fig. 4.5 and 4.6). Vascular spaces and Volkmann canals run from the marrow area to the periosteal bone (Fig. 4.6). Remnants of a destroyed Haversian system appear in Fig. 4.5.

Trabecular bone occupies 13% of the ratio and includes two different zones. A light layer (Fig. 4.2) between the inner compact bone and the medullar bone with few Volkmann canals (Fig. 4.4), and a most internal marrow area partially invaded by medullar bone. Secondary osteons are surrounded by lamellar tissue (Fig. 4.5). Frequent cavities (sometimes curved) formed by the enlargement of the Volkmann canals present mineral deposits with centrifugal growing (Fig. 4.6).

Preservation state. A series of fractures can be distin-

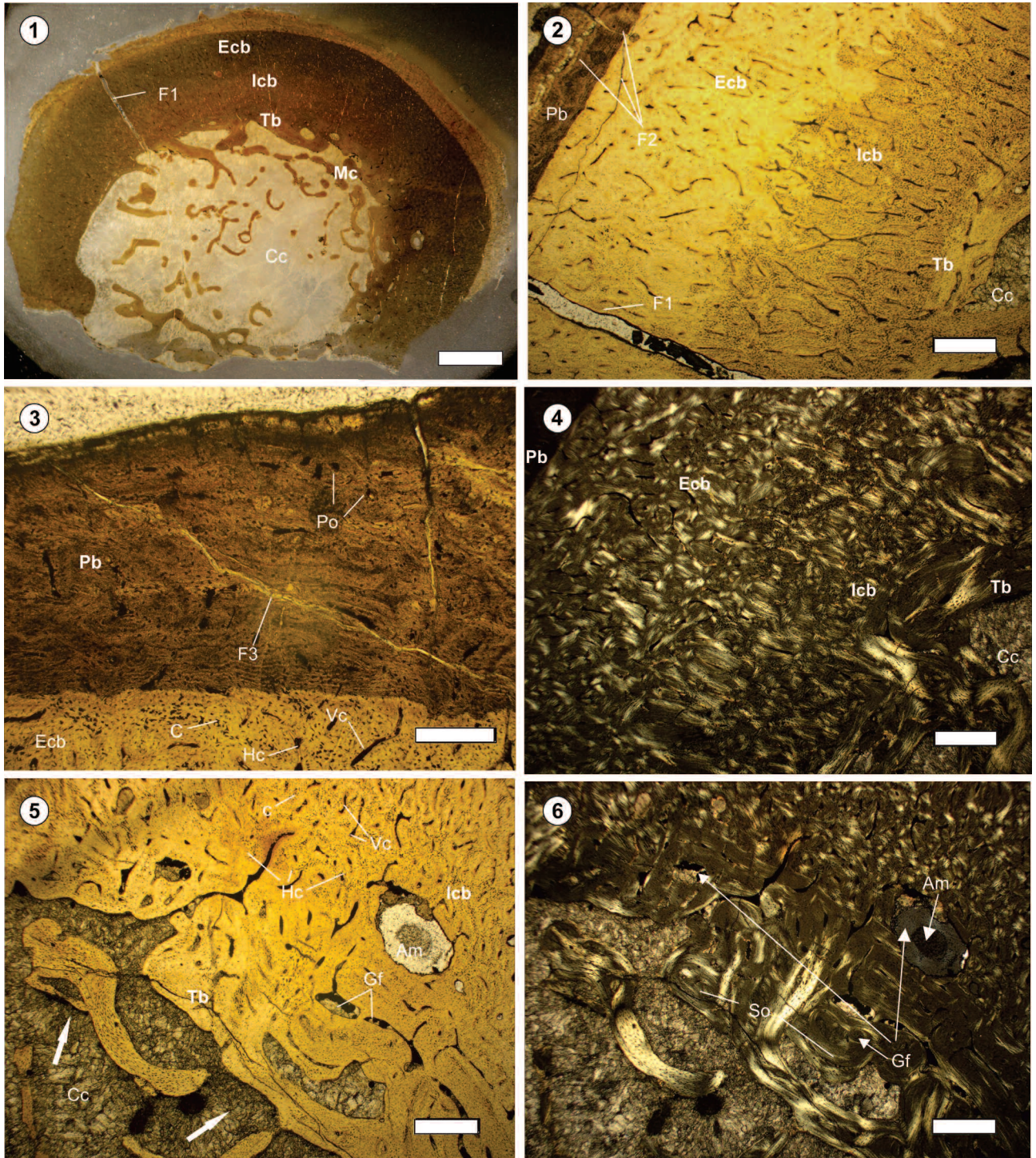


Figure 4. Transverse sections in a diaphysis of *Crossvallia unienwillia*. 1, Relationship between medullar spaces and the different layers of bone; 2, Detail of the proportions between the bone layers (Pb, Ecb, Icb and Tb), F1 running through the Pb and Icb, F2 running horizontally between the Pb and Ecb; 3, compact periosteal bone and detail of the Ft with fractures; 4, compact bone and detail of the fibers organization; 5, Icb with empty and very developed Vc, Hc, see the C density, Tb with spaces filled by Cc, the arrows signals the growing direction of carbonatic cement (Cc); 6, secondary osteons surrounded by lamellar tissue and carbonate minerals with Gf, the amorphous compound in the large cavities originated by resorption, characteristic of the molt cycles. Image (1) was taken with a binocular microscope, (2-6) were taken with a petrographic microscope; (4 and 6) taken with plane-polarizer (pp) and (2, 3, 5) without plane-polarizer (wp). Abbreviations: **Pb**, periosteal bone; **Ecb**, external compact bone; **Icb**, inner compact bone; **Tb**, trabecular bone; **Mc**, marrow cavity; **C**, canaliculi; **Po**, primary osteons; **So**, secondary osteons; **F1**, fracture 1; **F2**, fracture 2; **F3**, fracture 3; **Ft**, fibrolamellar tissue; **Am**, amorphous mineral; **Hc**, Haversian canals; **Vc**, Volkmann canals; **Cc**, carbonatic cement; **Gf**, geopetal filled. Scale bars= 20 mm (1), 100 µm (3), 200 µm (2, 3, 5, 6).

guished in the image analyzed without plane-polarizer (Fig. 4.2, 4.3). The most conspicuous one (Fig. 4.2) is located at the left lower corner, showing a diaclose morphology (F1) and runs across the complete section of the bone reaching the marrow space (Fig. 4.1). This central space is partially filled by carbonates with fibrous or granular textures (Fig. 4.5, 4.6). Radial fractures observed in the left upper corner (Fig. 4.2) cut across the compact periosteal bone layer, reaching the most peripheral cancellous bone, where it changes direction becoming tangential to the concentric layers (F2). A set of minor fractures starting from F2 (in the periosteal bone layer) taking then an opposite direction. A very compact fraction of periosteal bone (Pb) can be distinguished in the external portion of the bone. It is damaged by corrosion, with peeling signs on its external part and fractures subparallel (F3) to the layers of the fibro-lamellar tissue (Ft) filled by mineral compounds, (Fig. 4.3).

The middle part of the bone (Fig. 4.2) is represented by external compact bone (Ecb) with a few narrow canaliculi (c), some of them filled by mineral compounds (Cc). On the contrary (Fig. 4.5), the inner compact bone (Icb) is crossed by many thick canaliculi completely filled by carbonatic cement (Cc). The deepest osteological tissue (Fig. 4.5), identified as trabecular compact bone (Tb), leaves wide empty spaces completely obliterated by mineral cement (Cc). Under polarized light, the same image allows identifying fiber organization (Fig. 4.4, 4.6) showing the highest density of the external portion of compact bone (Fig. 4.4), and the highest porosity of the inner compact bone (Fig. 4.6). Also, the high bi-refringence of the carbonate cement (Cc) allows the individualization of the filled inner spaces of the fossilized bone (Fig. 4.6). The filling presents a geopetal texture mainly in the cancellous bone spaces (external marrow portion), and the fractures described above.

The same thin section observed without polarizing light

(Fig. 4.2) shows empty Canaliculi (C), Volkmann canals (Vc), and Haversian canals (Hc) in the Ecb (Fig. 4.3), whereas these structures are filled by Cc in the Icb and Tb (Fig. 4.5). The Cc appears in two forms, *i.e.*, as geopetal-coating with small crystals and as well-developed subhedral sparite-type crystals in the inner intertrabecular space. The Cc exhibits a centrifugal growth, decreasing in abundance toward the external section (Gf in Fig. 4.6). Observations under polarized light allowed verification of the compounds and the presence of empty spaces (isotropic components). The Cc presents two different textures. Crystals are tiny in the inner walls of the spaces with trabecular tissue. However, crystals are large in the central marrow cavity. Subhedral crystals have a centrifugal growth like those described above (Fig. 4.6).

Scanning Electron Microscope (SEM)

Secondary Electrons. The light gray area (Fig. 5.1) corresponds to osteological tissues. No empty spaces are observed, bone appears compact in section and the sub-circular inner area is filled by mineral deposits obliterating the marrow area of the pneumatic bone. Periosteal bone is diagenetically altered (see the pitted margin); a fracture with a clear filling of gypsum plates can be observed at the left (Fig. 5.2). This gypsum grows fibro-lamellarly between the bone and the inner fill in the medullar cavity.

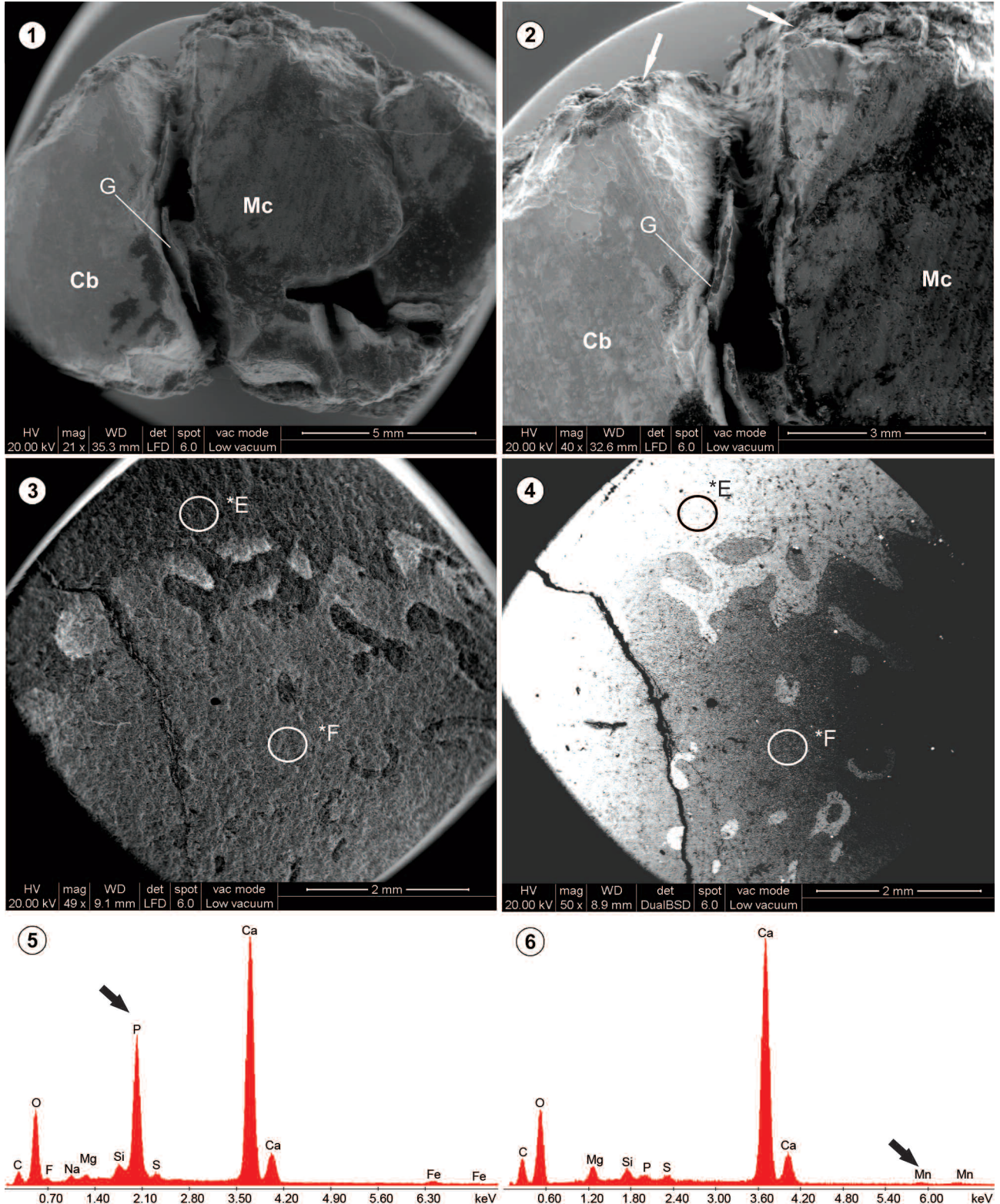
Backscattered electrons. Comparing the image observed with secondary electron and backscattered electron modes in figures 5C and 5D respectively, two large well defined areas can be distinguished regarding the atomic concentration in the sample (see Galván Josa *et al.*, 2013). The light gray area represents the mineral fill in the medullar space (Fig. 5.3). Dark gray portions correspond to compact bone and to the fill obliterating the inner spaces (marrow cavities); the rest of the area corresponds to medullar bone (lower part of the image, Fig. 5.4). Fractures appear in black color running

Figure 5. 1, Transverse sections of a long bone under SEM. Marrow cavity (Mc) fill and a large fracture with a mineral of laminar growth inside; **2**, Detail of the same image taken with Secondary Electrons. The light gray area corresponds to the compact bone (Cb), the dark gray central cylinder is the fill of the medullary space, the gypsum plate (G) is into the fracture. The arrows indicate the pitted margin in the external surface of the bone; **3**, Thin section of long bone with secondary electrons. External sector of bony fabric and small "islands" in the medullar space rounded by a mineral matrix; **4**, The same image done with backscattered electron mode, variations in tonality represent each different material. Light gray region is bone, whereas the dark gray represents the fill of medullar space (fractures and holes are in black); **5**, EDAX analysis of the external sector of the thin section, phosphorus corresponds to the chemical composition of the bone (see the arrow); **6**, EDAX analysis of the internal sector of the thin section, phosphorus disappears and Manganese belonging to the carbonate fill increases (see the arrow). Abbreviations: **Cb**, compact bone; **G**, gypsum. Scale bars= 5 mm (1), 3 mm (2), 2 mm (3, 4).

along the periosteal and compact layers; the little punctuated area represent the Haversian canals (and the enlarged cavities) and diaclasses. Brighter white dots correspond to

indeterminate minerals with a higher atomic density (Fig. 5.4).

EDAX. The microanalysis of electrons (EDAX) made on the



external portion of the bone (see Fig. 5.5) in the same sample previously observed in SEM indicates the presence of chemical elements mostly represented by calcium, phosphorus and oxygen characteristic of bone hydroxyapatite ($\text{Ca}_5(\text{PO}_4)_3\text{OH}$ or $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$). There is also a minor proportion of sulfur, fluorine and other subordinate complementary elements such as carbon, silica, magnesium, sodium, and iron in decreasing abundance (Fig. 5.5). In the inner portion, phosphorus is scarce and fluorine and sodium are totally absent (Fig. 5.6). Among the complementary elements, magnesium is poorly represented while iron disappears and is substituted by manganese. They mostly correspond to the carbonate-calcite CaCO_3 /dolomite $\text{CaMg}(\text{CO}_3)_2$ and manganocalcite $(\text{CaMn})\text{CO}_3$ - filling the inner portion of the bone.

X-ray

A complex series is formed by the varieties of Apatite in which the replacement of F^- , Cl^- and OH^- took place (Klein and Hurlbut, 1997). "Colofana" is the denomination of a dense and compact or cryptocrystalline variety of fluorapatite - $\text{Ca}_5(\text{PO}_4)_3\text{F}$ - present in fossil bones. It can take impurities or small quantities of calcium carbonate (Klein and Hurlbut, 1997) and combines as a solid solution with hydroxyapatite ($\text{Ca}_5(\text{PO}_4)_3\text{OH}$ or $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$) in biological matrices of original bones.

The following minerals appear in the diffractogram (mentioned in the prevalence order): fluorapatite "FAP" $\text{Ca}_5(\text{PO}_4)_3\text{F}$ and manganocalcite "MnCa" $(\text{Ca},\text{Mn})\text{CO}_3$, gypsum "Y" $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ (only in the Paleocene sample of *Crossvallia*), quartz "Q" SiO_2 and K-feldspar "FK" KAlSi_3O_8 . A good crystallinity is observed in phosphates (Fig. 6.1), higher than that of the Antarctic fossil *Spheniscus* (Jadwiszczak *et al.*, 2013b) and other minerals (mainly MnCa).

The diffractogram of the Eocene sample (*Spheniscidae* *indet.*) from Marambio (Seymour Island) shows a clear predominance of FAP and traces of Q. Crystallinity is similar to that in *Crossvallia* (Fig. 6.2).

In the fresh bone of extant *Pygoscelis adeliae* collected

at the same locality there is a variety of apatite "Ap" $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$, usually hydroxyapatite (Montel *et al.*, 1981) normally called "biogenic apatite or bioapatite", with a high content of organic matter. It is related to the poor crystallinity exhibited (Fig. 6.3).

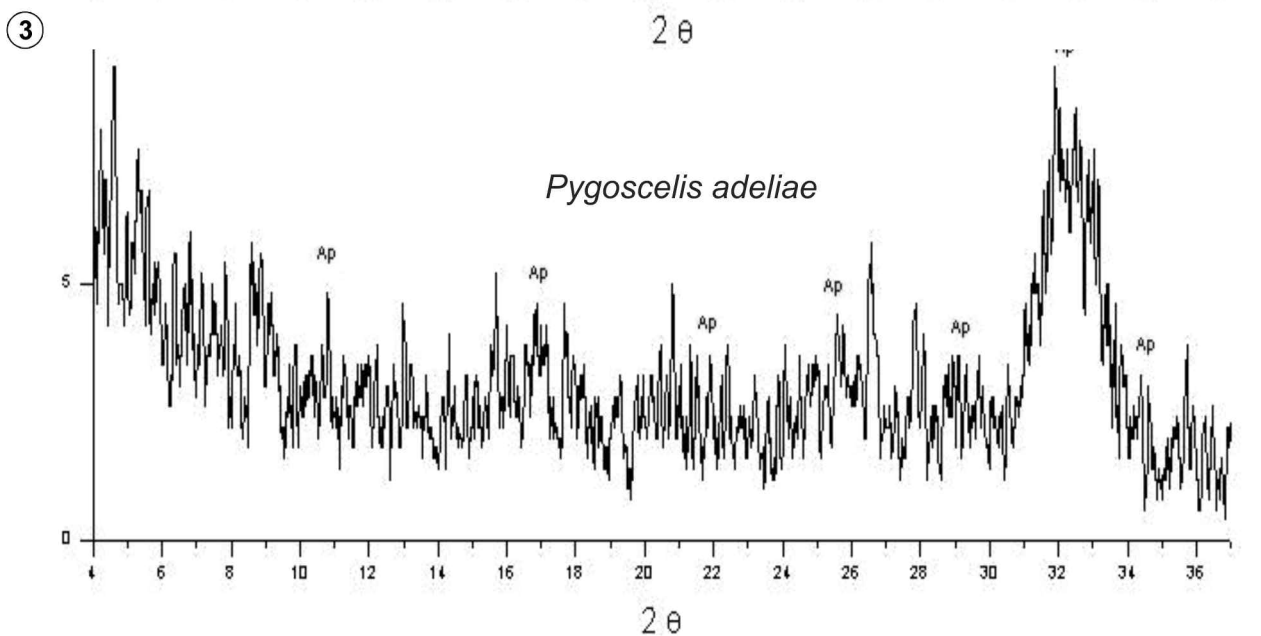
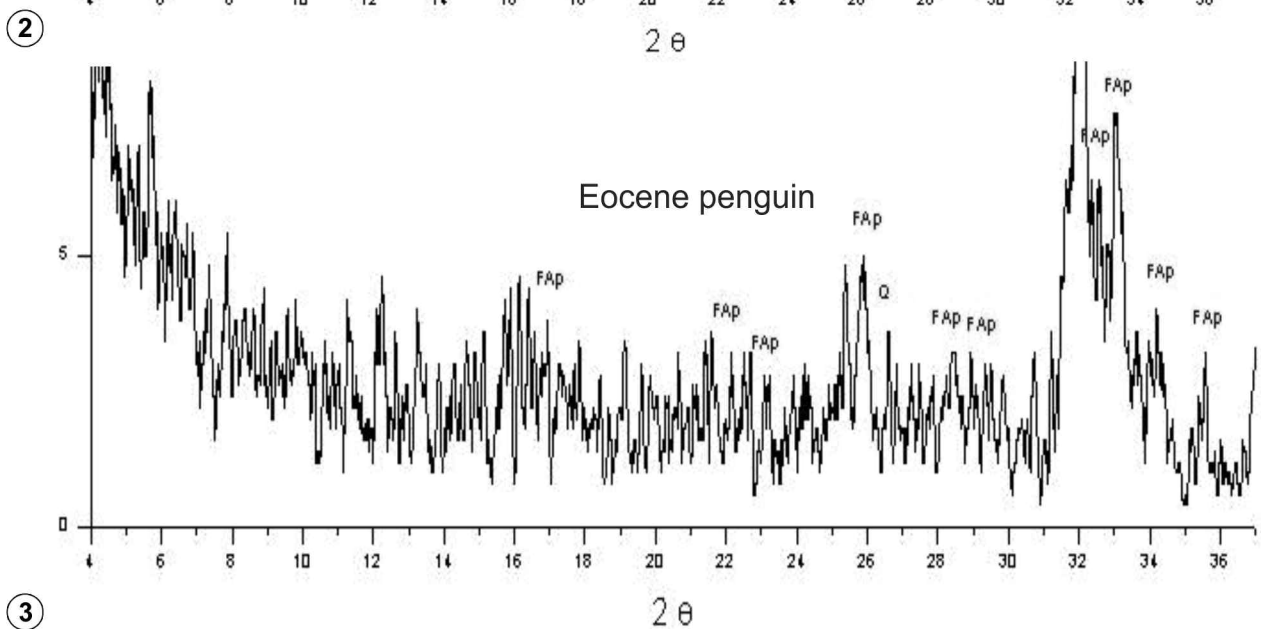
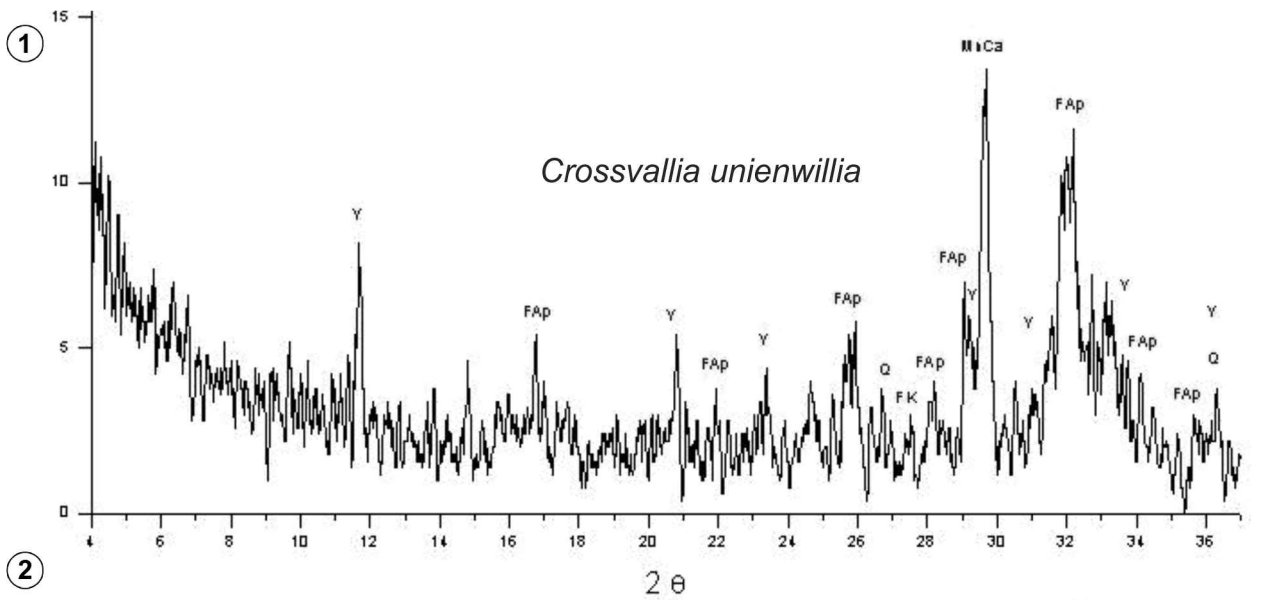
DISCUSSION

The fossil record of the Cross Valley Formation was strongly constrained by biostratigraphic and fossil diagenetic processes. These left an easily recognizable imprint in the remains of *Crossvallia*, partially destroying other fossil evidence as well. Apart from the plant remains preserved in the upper part of the Allomember C, a few fossil bones, shark and fish teeth, gastropods, bivalves and crinoids are the only body fossils preserved in this unit (see also Tambussi *et al.*, 2005; p. 668).

The preliminary appraisal during macroscopic analysis indicates that the holotype of *Crossvallia unienwillia* was badly preserved; fossil bones appear in several pieces with altered surfaces (Tambussi *et al.*, 2005). However, geochemical studies and microscopic analyses reveal that composition and tissular structure were preserved, allowing further interpretations on preservation in this single bearing penguin level.

The lithological features of the Cross Valley Allomember C record a range of depositional settings from shallow marine to delta plain environments arranged in a shallowing-upward trend. The erosional surface and the coarse-grained (breccia) deposits at the base of the upper allomember suggest an initial period of erosion and reworking of the underlying sediments. The fossil-bearing gray mudstones with marine invertebrates suggest a marine environment either below wave base or protected from wave action (such as a coastal lagoon). The upper sandstones and mudstones lack marine fossils but contain fossil wood, leaves and other plant debris that suggest a deltaic environment. Overall Allomember C is thought to represent deposition during a transgressive-regressive cycle.

Figure 6. Comparison of Rx diffractograms of selected penguin bones; **1**, Paleocene *Crossvallia unienwillia* (see the fluorapatite with a good crystallinity); **2**, Eocene *Spheniscidae* *indet.*, (see the fluorapatite also with a good crystallinity but without accessory minerals); **3**, The extant *Pygoscelis adeliae* (see the bioapatite with a low crystallinity).



Taphonomic history

The taphonomic pathway of *Crossvallia* was interpreted taking into account the mode of life of penguins. Considering that *Crossvallia* was a diving bird, we divided the taphonomic processes following Lawrence (1968; see however Fernández-López, 1988 for a different criterion).

Biostratinomy.- Considering the spatial relationships among skeletal elements in the field, *Crossvallia* represents a typically parautochthonous record (Fig. 2). Fossils were found disarticulated but associated (according to Behrensmeyer, 1991). The association of the skeletal elements in an area of approximately 1 m² (see Tambussi *et al.*, 2005) suggests only minor transport of the remains (Fig. 2). The apparent rapid burial is suggested also by the absence of signs of weathering and abrasion of the periosteal bone. By contrast, the lack of representation of any other element of this skeleton can be explained by fossil-diagenetic destruction (see conclusions below). The accompanying fish remains were also found isolated and are badly preserved as well.

The absence of longitudinal fractures, eyelet fractures or periosteal bone damage in *Crossvallia* indicates that weathering did not affect bones before burial (between stages 0/1 of Behrensmeyer, 1978). Moreover, previous disarticulation followed by early burial are also interpreted from the absence of irregular fractures produced when collagen was still a constituting part of the bone as in modern skeletons (see example of fractures in penguin bones in Acosta Hospitaleche *et al.*, 2012).

Fossil-diagenesis.- The transverse or oblique disposition of the fractures described above respect to the osteological tissue fibers suggests that they had a fossil-diagenetic origin. Damage described in the tibiotarsal and femoral epiphyses, diaphysis filling, corrosive deterioration of surfaces, mineral attachments (coating) of sulfates (gypsum), and siliceous grains preserving the bone morphology after dissolution were a consequence of geochemical processes occurring during burial and fossil-diagenetic time. The dissolution of surficial grains occurred by contact between elements of different chemical composition (bioapatite of phosphatic bone and quartzose siliceous sediment) and produced a material replacement keeping the original morphology.

Regarding the inner structure, there is no replacement of tissue composition. A normal interference color in the

petrographic sections indicates the preservation of the original bioapatite. Carbonate cement fills the inner spaces as coating on the walls and as crystals in the central area. A centrifugal growth of these fillings suggests that solutions percolated through diagenetic fractures (Fig. 4.6). Sulphate deposits (gypsum- anhydrite) observed in SEM images (Fig. 5.2) account for the acceleration of the destruction of the remains due to their expansionary growing force. Gypsum was already described as late cement formed during telogenesis in sandstones of the overlying La Meseta Formation (Marenssi and Net, 1999). Breakage of clasts by growing of expansive calcite cement was also described for the Cross Valley and Sobral sandstones (Marenssi *et al.*, 2012). In addition, the wedge action of ice, normal in the Antarctic seasonal dynamics, might have promoted further destruction of the materials at or near the present-day surface. It could also produce the initial fracture and crackling of bones, resulting in numerous little and indeterminate bony fragments as those mentioned above associated to the holotype.

The fossil-diagenesis in marine environments facilitates the replacement of OH⁻ by F⁻ (Jadwiszczak *et al.*, 2013b). That produced the changes in the apatite series as explained above. In the particular case of *Crossvallia*, increasing substitution is given by fluorine released by leaching of volcanoclastic sediments of the Cross Valley Formation. The cristallinity of Apatite, indicated by sharp peaks in the Rx (Fig. 6.1), would be the product of fossilization of the remains (see Jadwiszczak *et al.*, 2013b). Consequently, it is low in the fresh bone sample (see Fig. 6.3).

The manganocalcite filling of the inner spaces in *Crossvallia* would have precipitated during burial. The fractures passing through the periosteal layer to the medullar space were filled by gypsum, a late precipitate, probably near to the surface. The alternate presence/absence of water would have produced the destruction of bones by successive events of gypsum expansion/contraction. Differences in the atomic densities between bone and filling are evident in the backscattered electron mode (Fig. 5.4).

Palaeobiological considerations

Beyond the taphonomic scope of this paper, a few interesting findings about the specimen under study deserve some comments. Firstly, the fossils analyzed belong to an

undeniably diving bird, although the degree of specialization seems lower respect to other penguins, whether fossil or modern species. It is particularly interesting because the pachyostosis (in this case, pachyosteosclerosis) is a non-pathological modification of the bone, directly related with the underwater skills. It can be measured comparing the total thickness of the bone, which occupies 51% in *Crossvallia* (this paper), 55% in other Paleogene species such as *Palaeudyptes/Anthropornis*, and 57% in the Neogene *Spheniscus uribinai* (Yury-Yañez *et al.*, 2012). Results are consistent with the chronostratigraphic occurrence of the compared remains, and the expected trend of specialization for diving.

Another interesting and unexpected result is the presence of large resorption cavities found in the cortical bone definitely related to molt cycles (Fig. 4.5). The compact bone undergoes a series of changes during the molt cycle, correlated with the increasing need for calcium. It involves the enlargement of the Haversian system producing cavities by erosion and resorption of the bone substance followed by a deposition of new bone and formation of a new Haversian system (Meister, 1951; Kuenzel, 2003).

The cavities and the accompanying secondary osteons suggests that MLP 00-I-1-16 was an adult penguin that had molted more than once. Consistent with this idea is the thickness of the outer periosteal layer (Fig. 4.6) indicating that MLP 00-I-1-16 was a mature bird.

Besides, and despite widespread and persistent discussion about the medullary bone in reptiles (Schweitzer *et al.* 2007, Prondvai and Stein, 2014), there is consensus about its meaning in birds (Meister 1951, Chinsamy *et al.*, 2013). This tissue is only present in reproductively active females. Several studies demonstrated that medullary bone is directly related to the maturation of the ovarian follicles before egg laying, working as a calcium reservoir for the production of the calcareous eggshell (Dacke *et al.*, 1993). We interpret as medullary bone the trabecular tissue invading the medullary space (Fig. 4.1, 4.5). It implies that the specimen under study would have passed through at least one ovulating period before death.

CONCLUSIONS

Given the evidence presented here, this specimen of *Crossvallia unienwillia* is interpreted as an adult female that

underwent several molting periods; it was adapted to diving, albeit not as extremely adapted as the modern species. Fossil bones of *Crossvallia* are associated with a typical marine assemblage including sharks and macroinvertebrates in the Cross Valley C Allomember (former Bahía Pingüino Member, Tambussi *et al.*, 2005). The hosting mudstone suggests a low-energy environment either below the wave-base (prodelta) or protected from the wave action (lagoon or inter-distributary bay). In any case initial marine conditions changed to another with regular influx of land-derived (woods and leaves) material (Marenssi *et al.*, 2012).

The constrained spatial distribution and the preservational features described for remains of *Crossvallia* suggest biostratigraphic processes consistent with little transport and rapid burial, which would have prevented the action of destructive processes such as weathering and predation. The rapid burial favored the initial preservation of the elements under anoxic conditions. This is supported by the presence of manganocalcite observed in the diffractogram (developed under anoxic conditions) and by the bone tissue structure, the state of the epiphysis, and the preservation of the periosteal bone. The OH⁻ of the original hydroxyapatite (Ca₅(PO₄)₃OH) commonly known as bioapatite in the bones, was substituted by F⁻ and preserved as fluoroapatite (Ca₅(PO₄)₃F), which provided a higher resistance to destruction by chemical corrosion or mineral replacement.

The surficial corrosion, fractures, and the internal filling of the cavities suggest that destructive processes were only important after final burial during the telodiagenetic stage. The absence of more vertebrate fossil remains, including other parts of the *Crossvallia* skeleton, in the Cross Valley C Allomember could be the result of those processes, whereas on the contrary, the original depositional environment appears to be optimal.

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