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The fossil invertebrate marine fauna of the Gaiman Formation (Lower Miocene) at Bryn Gwyn (Chubut, Patagonia, Argentina)

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THE FOSSIL INVERTEBRATE MARINE FAUNA OF THE GAIMAN FORMATION (LOWER MIOCENE) AT BRYN GWYN (CHUBUT, PATAGONIA, ARGENTINA)

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Abstract. The Bryn Gwyn (Chubut Province, Patagonia, Argentina) is a classic fossiliferous site, long recognised for its Cenozoic vertebrate record. However, its invertebrate content remains poorly documented. The Lower Miocene Gaiman Formation, representing the "Patagonian Transgression", has yielded abundant vertebrates, whereas invertebrate faunas were historically mentioned only briefly, mostly as molds. New material was collected following the most recent stratigraphical framework at the Bryn Gwyn locality. Fossiliferous levels were identified, and several specimens were described and studied using updated systematic arrangements. The Bryn Gwyn fossil invertebrate assemblage previously comprised only 11 taxa and a few higher-level groups. Our new study documents 27 genera or species-level taxa, nearly doubling the known diversity. A new species, namely *Buccinanops halleri* sp. nov., is also described. Several groups previously reported without precise determinations (*e.g.*, bryozoans, gastropods, irregular echinoids) are now taxonomically resolved, and two additional higher-level groups, Brachiopoda and Scaphopoda, are recorded for the first time in the region. Comparisons with other Patagonian Cenozoic assemblages reveal strong faunal affinities with the time-equivalent Chenque and Monte León formations. These results substantially refine the taxonomic composition of the Bryn Gwyn invertebrate fossil fauna and provide a stronger basis for its inclusion in regional biostratigraphic correlations and paleoenvironmental reconstructions of the "Patagonian Transgression".

Key words. Bivalvia. Gaiman Formation. Gastropoda. Invertebrates. Miocene.

Resumen. LA FAUNA DE INVERTEBRADOS MARINOS FÓSILES DE LA FORMACIÓN GAIMAN (MIOCENO INFERIOR) EN BRYN GWYN (CHUBUT, PATAGONIA, ARGENTINA). El yacimiento de Bryn Gwyn (Provincia de Chubut, Patagonia, Argentina) es un yacimiento fosilífero clásico, conocido desde hace tiempo por sus registros de vertebrados del Cenozoico, pero con información fragmentaria sobre su contenido de invertebrados fósiles. La Formación Gaiman, que representa la "Transgresión Patagoniana" (Mioceno Temprano), ha proporcionado abundantes vertebrados, mientras que las faunas de invertebrados se han limitado históricamente a breves menciones, en su mayoría basadas en moldes. Nuevo material de invertebrados fósiles fue colectado siguiendo el marco estratigráfico más reciente en la localidad de Bryn Gwyn. Se identificaron los niveles fosilíferos y se describieron especímenes utilizando arreglos sistemáticos modernos. La asociación de invertebrados fósiles de Bryn Gwyn comprendía anteriormente solo 11 taxones y unos pocos grupos de rango taxonómico alto. Este trabajo documenta 27 géneros o taxones de nivel especie, lo que prácticamente duplica la diversidad conocida. Una nueva especie es descrita, *Buccinanops halleri* sp. nov. Varios grupos previamente descritos sin determinaciones precisas (por ejemplo, briozoos, gasterópodos, equinoideos irregulares) ahora se encuentran taxonómicamente resueltos, y se registran por primera vez dos grupos de alto rango taxonómico adicionales, Brachiopoda y Scaphopoda. Las comparaciones con otras asociaciones cenozoicas de la Patagonia revelan fuertes afinidades faunísticas con aquellas presentes en las formaciones Chenque y Monte León, ambas depositadas durante el Mioceno temprano. Estos resultados refinan sustancialmente la composición taxonómica de la fauna de invertebrados fósiles de Bryn Gwyn y proporcionan una base sólida para su incorporación en las correlaciones bioestratigráficas regionales y las reconstrucciones paleoambientales de la "Transgresión Patagoniense".

Palabras clave. Bivalvia. Formación Gaiman. Gastropoda. Invertebrados. Mioceno.

INTRODUCTION

Bryn Gwyn is a classic fossiliferous locality known for more than a hundred years (Ameghino, 1901; Windhausen, 1921). It is an important source of information about vertebrate faunas of South America during Cenozoic times. Bryn Gwyn is located in the southern margin of the lower Chubut River Valley, 8 km south of Gaiman city (Chubut), where Cenozoic sedimentary deposits are widely exposed.

The sedimentary succession comprises the Sarmiento, Gaiman, and Puerto Madryn formations, which range in late Eocene to the Late Miocene. Sediments deposited during a marine transgression informally known as "Patagonian Transgression" or "Patagoniense" (Feruglio, 1949; Parras & Cuitiño, 2021) are included in the Gaiman Formation.

The Gaiman Formation at Bryn Gwyn is well known for its abundant and diverse fossil record of marine vertebrates, collected during several decades since the pioneering work of Simpson (1935). This record includes cetaceans (*e.g.*, Buono et al., 2017; Viglino et al., 2018, 2019; Paolucci et al., 2021), birds (*e.g.*, Cione et al., 2011; Piro & Acosta Hospitaleche, 2022; Tambussi et al., 2023), turtles (Sterli et al., 2025), and fishes (*e.g.*, Cione, 1978; Cione & Azpelicueta, 2003; Cione et al., 2011). Unlike fossil vertebrates, and despite their abundance, fossil invertebrates are less known in this area. They are usually mentioned in lithostratigraphic descriptions (*e.g.*, Cuitiño et al., 2019), but are always considered a minor component of the fossil assemblages. Furthermore, most of these mentions referred to fossil invertebrates only as molds (see below), and no systematic descriptions have been performed for the invertebrate fossils from this locality thus far.

Fossil invertebrates at Bryn Gwyn were first mentioned by Ihering (1904, 1907), who indicated the presence of bivalves, gastropods, and echinoderms. He listed the species *Ostrea patagonica* d'Orbigny, 1839, *Chione patagonica* (Ihering, 1897), *Martesia patagonica* (Philippi, 1887), *Turritella ambulacrum pyramidesia* Ihering, 1907, and *Monophora darwini* Desor, 1847. Ihering (1904, 1907) considered this fauna similar to that found in Península Valdés and surrounding areas, today referred to as the Puerto Madryn Formation ('Entrerriense' for the author). Frenguelli (1927, 1935) expanded the list, adding *Ostrea hatcheri* Ortmann, 1897, *Pectunculus cuevensis* Ihering, 1897, *Sanguinolaria perplana* (Ihering, 1897), *Polinices* sp., and *Turritella breantiana* d'Orbigny, 1846. In posterior geological and paleontological studies carried out in the area, only these mentioned species are indicated (Simpson, 1935; Feruglio, 1949). Camacho and Fernandez (1956) expanded the faunal list by adding *Venericardia* (*Venericor*) *austroplata* Gardner and Bowles, 1939, a taxon with an important biostratigraphic significance according to these authors. Later, only mentions of crabs (Haller & Mendía, 1980), pectinids, echinoids (Scasso & Castro, 1999), corals, and bryozoans (Cuitiño et al., 2019) were indicated. Several studies cited oysters, turritellids, and bivalve and gastropod molds (Lech et al., 2000; Scasso & Bellosi, 2004; Cuitiño et al., 2019). Recently, del Río et al. (2022a) referred to molds of pectinids, venerids, and pholadideans not yet identified for these horizons.

The recently published new geochronologic scheme for the Gaiman Formation (Cuitiño et al., 2023) motivated a new stratigraphically and chronologically constrained material collection, allowing us to perform the first detailed systematic research, including descriptions of the fossil invertebrates of the Gaiman Formation in the Bryn Gwyn area. This new fauna description allows comparisons with other better-known Miocene marine assemblages of Patagonia.

Institutional acronyms. CNP-PIIc, Colección de Paleoinvertebrados e Icnología, Instituto Patagónico de Geología y Paleontología, Centro Nacional Patagónico, Puerto Madryn, Argentina; **MPEF-PI,** Colección de Invertebrados, Museo Egidio Feruglio, Trelew, Argentina.

GEOLOGICAL SETTING

The studied material comes from Bryn Gwyn ('white cliff' in Welsh language), a locality situated in northeast Chubut Province, Argentina, at the southern margin of the Chubut River Valley, 8 km south of Gaiman city (Fig. 1). Cenozoic outcrops at this locality are considered as part of the Valdés Basin sedimentary infill (Cuitiño et al., 2023) and three stratigraphic units successively crop out: Sarmiento, Gaiman and Puerto Madryn formations. The Sarmiento Formation is a terrestrial tuffaceous succession divided into three members: the lower Pan de Azucar Member (Eocene), the middle Rojo Member (Eocene-Oligocene?), and the upper Trelew Member (Lower Miocene). At Bryn Gwyn, the Gaiman Formation lies on a regionally correlated surface (S2 *sensu* Cuitiño et al., 2023) on top of the Trelew Member of the Sarmiento Formation. In turn, the Gaiman Formation is covered by the Upper Miocene Puerto Madryn Formation, separated by another regionally extensive surface that comprises most of the Middle Miocene and is defined as S3 by Cuitiño et al. (2023). At Bryn Gwyn, the Puerto Madryn

Formation is composed of cross-bedded sandstones and a few mudstones with conspicuous oyster biostromes (Fig. 2).

Outcrops of the Gaiman Formation (Haller & Mendía, 1980) are common along the coastal cliffs of NE Chubut Province and the lower reaches of the Chubut River Valley (Scasso & Castro, 1999; Cuitiño et al., 2019, 2023). The unit is composed mostly of bioturbated, tuffaceous muddy sandstones, with minor mudstones and laminated fine sandstones. These deposits were interpreted as deposited in shallow marine paleoenvironments from the coastal zone to the inner shelf (Scasso & Castro, 1999; Cuitiño et al., 2019, 2023; Allende Mosquera et al., 2023; Farroni et al., 2023; Panti et al., 2025). The study area is one of the few places where the base and top of the Gaiman Formation are exposed, with a thickness of 70 m (Fig. 1).

The age of the Gaiman Formation is estimated based on stratigraphic correlation, zircon U-Pb geochronology, and age constraints from the underlying and overlying units. Based on its rich fossil terrestrial vertebrate fauna (Kay et al., 2008) and zircon U-Pb radiometric dates (Cuitiño et al., 2023), the underlying Trelew Member of the Sarmiento Formation was defined as Lower Miocene (~21 Ma); for this reason, the Gaiman Formation is no older than Burdigalian (Early Miocene). Zircon U-Pb ages from the Gaiman Formation beds from several localities of NE Chubut (including one at Bryn Gwyn, Fig. 2) support a Burdigalian age (Cuitiño et al., 2023). An Early Miocene age is also supported by the presence of extinct fish, penguins (Cione et al., 2011), and cetaceans (Buono et al., 2017; Viglino et al., 2018, 2019). The age of the uppermost beds of the Gaiman Formation is uncertain, although based on stratigraphic correlations and sedimentation rates, Cuitiño et al. (2023)

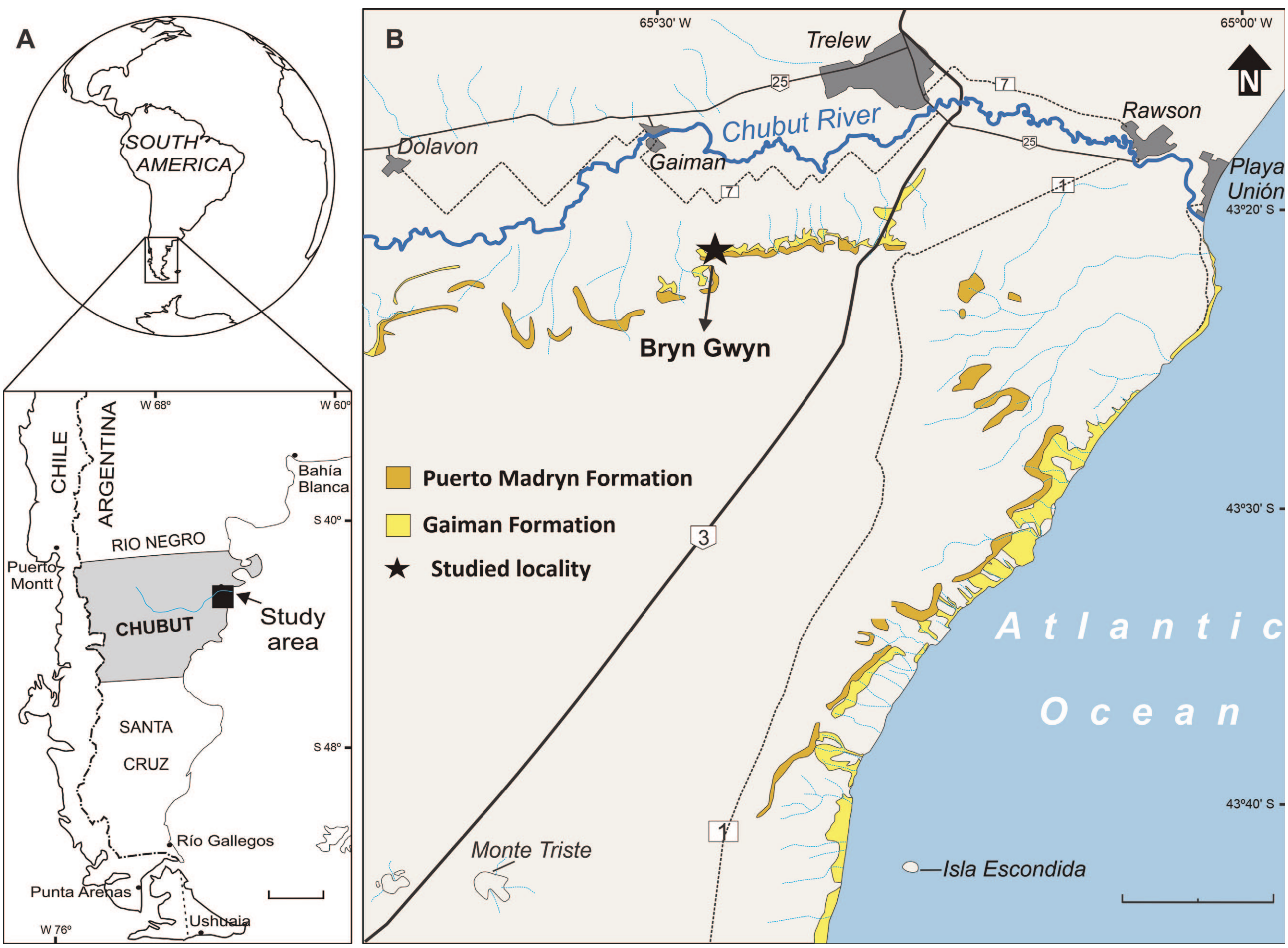


Figure 1. A, Regional location of the studied area. B, Detailed map of the studied area showing the distribution of Miocene sedimentary deposits. Modified from Cuitiño et al. (2019). Scale = 200 km (A), 10 km (B).

suggested the Gaiman Formation should not be younger than 16 Ma. The overlying Puerto Madryn Formation has been dated between 12 and 8 Ma in the Península Valdés area, indicating a Tortonian age (Late Miocene) (Scasso et al., 2001; del Río et al., 2018; Cuitiño et al., 2023).

At the regional scale, the Gaiman Formation is included in the informal local stage *Patagoniense* (Parras & Cuitiño, 2021), which broadly correlates with other similar Lower Miocene shallow marine sediments throughout eastern Patagonia (Monte León, Chenque, Gran Bajo del Gualicho formations, among others).

MATERIALS AND METHODS

Fossil material was collected at Bryn Gwyn locality and nearby areas during a stratigraphic and paleontological survey of the Gaiman Formation during several fieldworks from 2021 to 2024. As a base for field data collection, we used the stratigraphic section of Cuitiño et al. (in press). All beds were analysed, and those containing fossil invertebrates were labelled from base to top as level 1 to level 8 (Fig. 2). The best-preserved specimens were collected to be prepared and observed at the Instituto Patagónico de Geología y Paleontología laboratories. All material was viewed using a Leica binocular magnifying glass. Linguliformea systematics follows Williams et al. (2000). General Mollusca systematics followed MolluscaBase (2025). Bryozoa, Echinodermata, and Arthropoda systematics follow WoRMS (2025). Open nomenclature follows the proposals of Bengtson (1988). A similarity cluster analysis was performed in order to compare our resulting invertebrate assemblage with others from different Cenozoic marine stratigraphic units of Patagonia. For this, we perform a UPGMA distance analysis using the Bray-Curtis algorithm in PAST 4.03 (Hammer et al., 2001).

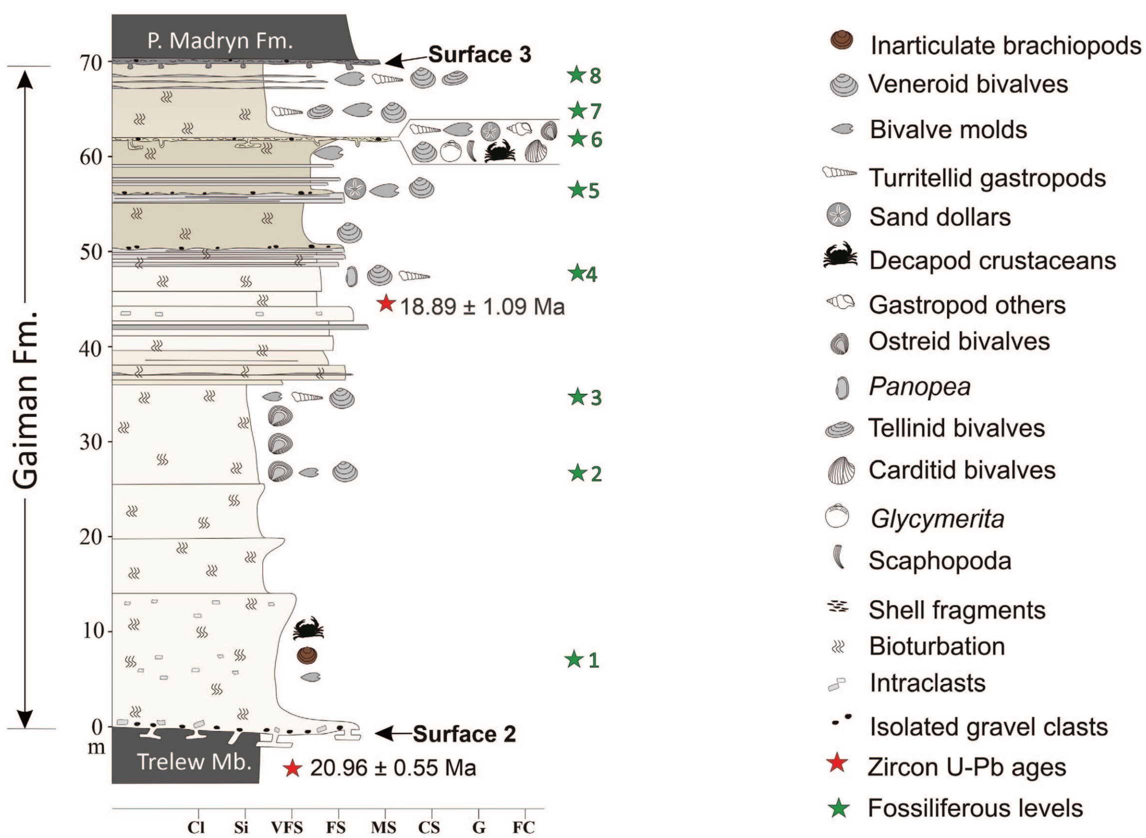


Figure 2. Sedimentary log of the Gaiman Formation at Bryn Gwyn (modified after Cuitiño et al., in press) showing the fossiliferous levels studied in this work. Zircon U-Pb ages and stratigraphic surface labels are from Cuitiño et al. (2023). Abbreviations: Cl, clay; CS, coarse sand; FC, fine conglomerate; FS, fine sand; G, gravel; MS, medium sand; Si, silt; VFS, very fine sand.

All specimens are housed in the Colección de Paleoinvertebrados e Icnología at the Instituto Patagónico de Geología y Paleontología (IPGP, CCT CONICET-CENPAT) in Puerto Madryn, Chubut Province, Argentina; and in the Colección de Invertebrados at Museo Egidio Feruglio (MEF), in Trelew, Chubut Province, Argentina.

SYSTEMATIC PALAEONTOLOGY

BRACHIOPODA Duméril, 1805
LINGULIDA Waagen, 1885
DISCINIDAE Gray, 1840

Genus ***Discinisca*** Dall, 1871

Type species. *Orbicula lamellosa* Broderip, 1833. Original designation. Recent, Ocean Pacific coast from Peru to Chile.

Discinisca porvenir Pérez, Farroni, Allende Mosquera and Cuitiño, 2023
Figure 3A, B

Referred material. Paratype CNP-PIIc 594, one dorsal valve (length= 27.3 mm, width= 21.8 mm, height= 8.3 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 1, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. *Discinisca porvenir* was recently described for the Gaiman Formation, together with *D. messii* Pérez, Farroni, Allende Mosquera and Cuitiño, 2023. More information about this species is provided by Pérez et al. (2023).

There are no previous records of brachiopods indicated for the Gaiman Formation. Lingulid, terebratulid, and rhynchonellid brachiopods are present in other Neogene units of Patagonia (Ihering, 1903; Frenguelli, 1927; Levy, 1961; Martínez et al., 2025). The group is present in the overlying Puerto Madryn Formation, represented by the lingulid *Lingula* sp. nov.? (Frenguelli, 1927) (*Glottidia*, according to Martínez et al., 2025), the terebratulid *Pachymagas piramidesia* (Ihering, 1903), and the abovementioned discinid *D. messii* (Pérez et al., 2023, 2024). Neogene discinid brachiopods are rare in South America, with only two mentions of Late Miocene age from Uruguay and the Entre Ríos Province (Figueiras, 1980; Pérez et al., 2013), and other possible records from Chile (Philippi, 1887).

BRYOZOA Duméril, 1805
CHEILOSTOMATIDA Busk, 1852
CUPULADRIIDAE Lagaaij, 1952

Genus ***Discoporella*** d'Orbigny, 1852

Type species. *Lunulites umbellata* Defrance, 1823 (= *Discoporella umbellata*). Original designation. Miocene–Recent, Eastern Atlantic.

Discoporella sp.
Figure 3C–E

Referred material. CNP-PIIc 1408, one colony (diameter= 6.85 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. This free-living bryozoan colony has a discoidal and flat shape, highly calcified, spiral growth pattern, circular to hexagonal zooids bordered by a strong ridge. Even though no other characters are visible in our material, the described characters allow us to consider it a representative of the cupuladriid genus *Discoporella* d'Orbigny, 1852 (Baluk & Radwański, 1982; Cook & Chimonides, 1994).

Cupuladriid bryozoans are known for several Cenozoic Patagonian units (López-Gappa et al., 2017). In particular, the genus *Discoporella* was mentioned for the overlying Puerto Madryn Formation (Casadío et al., 2005) and for the Late Miocene Camacho Formation of Uruguay (Closs & Madeira, 1968). In addition, there is a dubious mention of this genus as *Cupularia punctata*—synonym of *D. depressa* (Conrad, 1841)—by Canu (1904) from the "*Patagonien inférieur*" of "*Coli-Huapi*" (probably referring to outcrops of Chenque Formation).

GASTROPODA Cuvier, 1795
VETIGASTROPODA Salvini-Plawen, 1980
TROCHIDAE Rafinesque, 1815

Genus ***Molvaldesia*** del Río, 2022
(in Nielsen & del Río, 2022)

Type species. *Valdesia valdesiensis* del Río, 1985 (=*Molvaldesia valdesiensis*). Original designation. Late Miocene, Puerto Madryn Formation, Argentina.

Molvaldesia* cf. *M. astraensis (Morra and del Río, 1987)
Figure 3F–O

Referred material. CNP-PIIc 1409, 1423, seven specimens preserved as composite molds; diameter range: 9–21 mm (mean= 16.5 mm), height range: 6–13.95 mm (mean= 10.2 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. These specimens have conic, trochiform shells with low spire, deep sutures, and a subaquadrate to rhomboidal aperture. Sculpture is given by nearly 12 to 14 elongated and ophistocline nodes located in the upper portion of the whorls, a double peripheral carina, and 12–14 basal spiral cords. These features allow us to include these specimens in the genus *Molvaldesia* (=*Valdesia* del Río, 1985). Among the species of this genus, our shells resemble *M. astraensis* (Morra & del Río, 1987) (Chenque Formation, Chubut) in outline, the presence of a narrow sutural ramp, and the number and development of nodes. Another species, *M. leonardinii* (del Río, 1985), from the Puerto Madryn Formation (Chubut Province) has a nearly similar number of nodes and basal spiral cords, but differs in the presence of a higher spire, a less pronounced sutural ramp, and a more rounded development of the double peripheral carina. Other species such as *M. cuevensis* (Ihering, 1897); *M. camachoi* (del Río, 1985); or *M. valdesiensis* (del Río, 1985) differ in having higher spires. Variability in the number of sculptural elements among species is present in other trochid taxa. This suggests that a comprehensive quantitative revision of the genus is required. The variability present in this genus does not allow us to give a more precise taxonomic placement to our specimens.

Considering the general morphology of the specimens here described, we compare them to *M. astraensis*, although the different number of basal spiral cords left some doubts about this placement.

CAENOGASTROPODA Cox, 1960
NATICIDAE Guilding, 1834

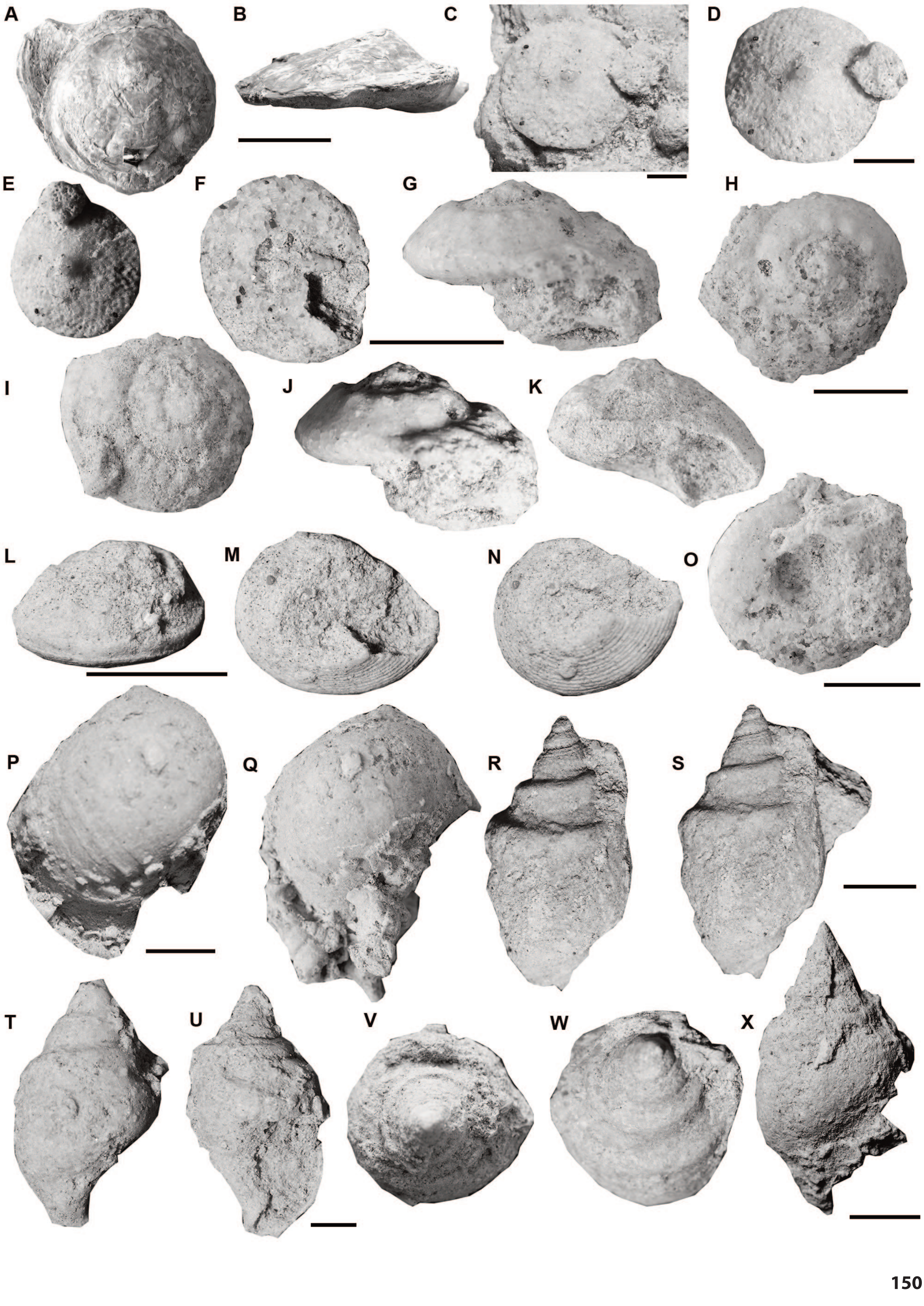
Genus ***Glossaulax*** Pilsbry, 1929

Type species. *Natica reclusiana* Deshayes, 1839 (= *Glossaulax reclusiana*). Original designation. Recent, Pacific coast of California, USA.

Glossaulax*? cf. *G. secundum
(Rochebrune and Mabille, 1885)
Figure 3P–Q

Referred material. CNP-PIIc 1410, 1425, six composite molds; diameter range: 32–40 mm (mean= 34.1 mm); height range: 20.9–33.4 mm (mean= 28.3 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. The taxonomy of fossil naticids is very complex because most of the diagnostic characters are based on non-fossilizable structures. Nevertheless, some genera also include features referred to the aperture, collumelar lips and umbilicus. Our material consists of composite molds clearly assignable to the Family Naticidae by their shell outline and the absence of shoulders in whorls. The umbilicus is present, but the aperture is missing in our specimens. Therefore, neither umbilical callus nor the groove incising the callus is visible. This does not allow to define a generic placement. Regardless, other characters, such as the spire height and the number and morphology of whorls, are similar to the species *Glossaulax secundum* (Rochebrune & Mabille, 1885). This species is variable but presents a medium-sized, globose, and thickened shell with a very low spire, the last whorl greatly inflated and rounded basally, and a smooth shell surface (Griffin & Pastorino, 2013). The absence of umbilical characters does not allow a more precise identification.

Figure 3. A–B, *Discinisca porvenir* Pérez et al., 2023, CNP-PIIc 594 (paratype); A, outer view of dorsal valve; B, left lateral view of dorsal valve; C–E, Colony of *Discoporella* sp., CNP-PIIc 1408; C, dorsal view of colony in sediment; D–E, detail of colony in dorsal view; F–O, *Molvaldesia* cf. *M. astraensis* (Morra and del Río, 1987), CNP-PIIc 1409; F, M–O umbilical view; G, K–L, apertural view; H–I, apical view; L, lateral view; P–Q, *Glossaulax*? cf. *G. secundum* (Rochebrune and Mabille, 1885), CNP-PIIc 1410; P, lateral view; Q, apertural view; R–X, *Buccinanops halleri* sp. nov.; R–S, CNP-PIIc 1411 (holotype), lateral views; T–X, CNP-PIIc 1412 (paratypes); T, X, lateral views; U, apertural view; V–W, apical views. Scale = 10 mm (A–B, F–Q), 5 mm (R–X), 2 mm (C–E).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The genus *Polinices* has been mentioned from the Gaiman Formation at the Bryn Gwyn area (Frenguelli, 1927, 1935) and probably refers to the taxon here revised.

Glossaulax secumdum occurs in other Early Miocene units, including San Julián, Monte León, Estancia 25 de Mayo, and Chenque formations (Griffin & Pastorino, 2013; Bostelmann et al., 2015). Brunet (1995) described two *Glossaulax* species from the Late Miocene of the Puerto Madryn Formation: *G. groeberi* and *G. keideli*. Griffin and Pastorino (2013) stated these species as junior synonyms of *G. secundum*.

BUCCINANOPSIDAE Galindo, Puillandre, Lozouet and Bouchet, 2016

Genus ***Buccinanops*** d'Orbigny, 1841

Type species. *Buccinum cochlidium* Dillwyn, 1817 (=*Buccinanops cochlidium*). Original designation. Holocene, Puerto Belgrano, Buenos Aires, Argentina (Ihering, 1907). Recent, Atlantic Ocean coast of South America, from Rio Grande do Sul, Brazil, to Puerto Madryn, Argentina (Pastorino & Simone, 2021).

Buccinanops halleri sp. nov.
Figures 3R–X, 4A–D

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Etymology. Specific name honours to Dr. Miguel Haller, an Argentinian geologist and professor, who recently passed away. Miguel Haller was the first to give a comprehensive description of the Gaiman Formation.

Type Material. Holotype CNP-PIIc 1411, one composite mold; diameter: 20.7 mm, height: 38.2 mm. Paratypes CNP-PIIc 1412 eighteen composite molds; diameter range: 9.9–27.8 mm (mean= 18.2 mm), height range: 16.6–49.8 mm (mean= 31.4 mm).

Referred Material. CNP-PIIc 1424, two specimens.

Diagnosis. Shell of medium size, smooth, with five to six whorls; spire low; shouldered whorls with marked subsutural flat cords without nodes or spines; teleoconch with thin well-marked spiral cords until the fourth whorl; two terminal columellar folds.

Description. Bucciniform and medium-sized shell with a maximum height of 49.8 mm. The teleoconch consists of five to six smooth whorls. Spire acute, equal or less than one third of the maximum shell height. Suture well-defined and impressed, narrow shouldered whorls always present. Marked subsutural flat cords without nodes or spines, more pronounced from the third to the fourth whorl. First teleoconch whorls (up to the fourth) with thin, well-marked spiral cords placed under subsutural cords. Parietal callus not visible. Aperture large, less than half of the total shell height with a distinct siphonal notch in the basal lip. Two marked terminal columellar folds.

Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Recently, Pastorino and Simone (2021) carried out an extensive review of living species of *Buccinanops*, splitting the genus into two: *Buccinanops* and *Buccinastrum* Pastorino and Simone, 2021. Main morphological differences between the two genera include larger shells for *Buccinanops*, with the presence of shallow shoulders frequently with subsutural flat cords in the last whorls, first teleoconch whorls not smooth, spire height equal or less than one-third of the total shell height, and weak terminal columellar folds. All of these characters are visible in our specimens, and thus, they are assigned to *Buccinanops*.

Pastorino and Simone (2021) included in *Buccinanops* three living species: *B. cochlidium* (Dillwyn, 1817), *B. latus* Pastorino and Simone, 2021, and *B. monilifer* (Kiener, 1834). A fourth fossil species is mentioned, *B. ellipticum* (Whitefield, 1865), from the Eocene of North America (Garvie, 1996). Nevertheless, *B. ellipcticum* presents an unusual outline for *Buccinanops* species, without shoulders or subsutural cords, and without columellar folds. Thus, the assignment of the North American species would require further revision.

Among living species, *B. halleri* sp. nov. resembles *B. cochlidium* in shell outline and development of the shoulders and subsutural cords but differs by its lower spire, absence of axial riblets, and presence of two well-marked terminal columellar folds. From *B. latus*, the new species can be distinguished by its less globose teleoconch and absence of axial riblets and subsutural nodes. *Buccinanops halleri* sp. nov. differs from *B. monilifer* by having a lower spire and by the absence of subsutural nodes or spines.

The fossil record of the genus *Buccinanops* is restricted to the Pleistocene–Holocene of Argentina, Uruguay, and Brazil (Ihering, 1907; de Mata, 1947; Lopes et al., 2013;

Rojas et al., 2018). Other records referred to this genus already indicate species that probably belong to *Buccinastrum* (Aguirre et al., 2006; Martínez et al., 2016; Agnolín et al., 2024). A complete revision of the Patagonian fossil record of *Buccinanops* and *Buccinastrum* under the new taxonomic approach of Pastorino and Simone (2021) is required. Based on this interpretation, *B. halleri* sp. nov. would represent the oldest undoubted record of the genus *Buccinanops* in Argentina.

Brunet (1995) indicated the occurrence of *Buccinanops* aff. *B. squalidum* (King, 1832)—*Buccinastrum paytense* (Kiener, 1834)—in the Puerto Madryn Formation. Development of the outline, spire, and whorls of this record are concordant with the genus *Buccinastrum*. Further studies on this material are required.

VOLUTIDAE Rafinesque, 1815
ODONTOCYMBIOLINAE Clench and Turner, 1964

Genus ***Miomelon*** Dall, 1907

Type species. *Volutilithes philippiana* Dall, 1890 (=*Miomelon philippianum*). Original designation. Recent, Pacific coast of Chile.

Miomelon gracilior (Ihering, 1896)
Figure 4E–F

Referred Material. CNP-PIIc 1418, two composite molds; diameter range: 13.6 mm, height range: 20.2–40.4 mm (mean: 30.3 mm) but one specimen incomplete.
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. The Family Volutidae is one of the gastropod groups most recognizable by its large shells (Stuardo & Villarroel, 1974). However, in the Gaiman Formation, only relatively small specimens of Volutidae are found. Systematics within Volutidae are, as in other gastropod families, mainly based on radular and protoconch characters, and a high grade of convergence is found in adult shells (Clench & Turner, 1964). In spite of this, Neogene South American volutids have been studied in the last decades (del Río & Martínez, 2006; Nielsen & Frassinetti, 2007).

The genus *Miomelon* is a long-lived taxon found since the late Oligocene of Argentina and Chile in southern South America (del Río & Martínez, 2006), and it is characterized by having a fusiform, small to large-sized shells, elevated spire, and a teleoconch sculptured by 10-22 axial costae and several spiral cords forming a reticulate pattern with the axial costae (Stuardo & Villarroel, 1974; del Río & Martínez, 2006). Despite the poor preserved condition of our material, all these characters are visible.

Among representatives of *Miomelon*, the species *M. gracilior* has a fusiform to elongate-fusiform shell, with spire comprising 35% to 50% of total length, suture strongly impressed, spiral cords of equal width, and axial costae extended from suture to suture (del Río & Martínez, 2006). The species has a very variable outline, with different development of the spire. In addition, spiral cords are always more conspicuous than axial costae. Our material shows these characters, and thus, it is assigned to *M. gracilior*. Other species of *Miomelon*, such as *M. dorbignyana* (Philippi, 1887) or *M. castilloensis* (Ortmann, 1900) has more conspicuous spiral cords and less marked axial elements (del Río & Martínez, 2006).

Miomelon gracilior is one of the most abundant and widespread volutid species in the Cenozoic marine sequences of Argentina (see del Río & Martínez, 2006). This species ranges from the Oligocene to the Early Miocene in southern South America, is found in San Julián, Monte León, Carmen Silva, and Estancia 25 de Mayo formations from Argentina, and in the Guadal Formation from Chile (Del Río & Martínez, 2006; Bostelmann et al., 2015). The record here provided extends the geographic range of the species to the Chubut Province and adds the Gaiman Formation to its known stratigraphic range.

Genus ***Pachycymbiola*** Ihering, 1907

Type species. *Voluta brasiliana* Lamarck, 1811 (= *Pachycymbiola brasiliana*). Original designation. Recent, Eastern Atlantic coast from Rio de Janeiro, Brazil, to Puerto Deseado, Argentina.

Pachycymbiola camachoi del Río and Martínez, 2006
Figure 4G–M

Referred Material. CNP-PIIc 1419, one composite mold, diameter: 17.8 mm, height: 37.5 mm; CNP-PIIc 1420, seven composite molds: diameter range: 21.2–39.3 mm (mean=

28.75 mm), height range: 36.9–54.4 mm (mean= 49.8 mm).

Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Particularities of the taxonomy of the Volutidae are indicated in the previous species remarks. The genus *Pachycymbiola* is known from the Early Miocene to Recent in southern South America, and it is characterized by its thick, medium to large-sized shells, with biconic to ovate outline, spire generally low, presence of peripheral tubercles, last whorl large and convex, frequently well-marked shoulder, and a broad siphonal notch (del Río & Martínez, 2006). Several specimens found in the Gaiman Formation match this description, and are, thus, assigned to the genus.

Our specimens also show a slender and biconic outline, with relatively high spire and well-marked peripheral tubercles perpendicularly projected and bordering of the sutural ramp. These features characterized the species *P. camachoi*, previously found in the coeval Gran Bajo del Gualicho and Chenque formations (del Río & Martínez, 2006).

STRUTHIOLARIIDAE Fischer, 1884

Genus ***Perissodonta*** Martens, 1878

Type species. *Struthiolaria mirabilis* Smith, 1875 (=*Perissodonta mirabilis*). Original designation. Recent, Kerguelen Islands.

Perissodonta ameghinoi (Ihering, 1897)
Figure 4N–R

Referred Material. CNP-PIIc 1426, three composite molds; diameter range: 16.7–22.5 mm (mean= 19.4 mm), height range: 22.7–30 mm (mean= 26.4 mm).

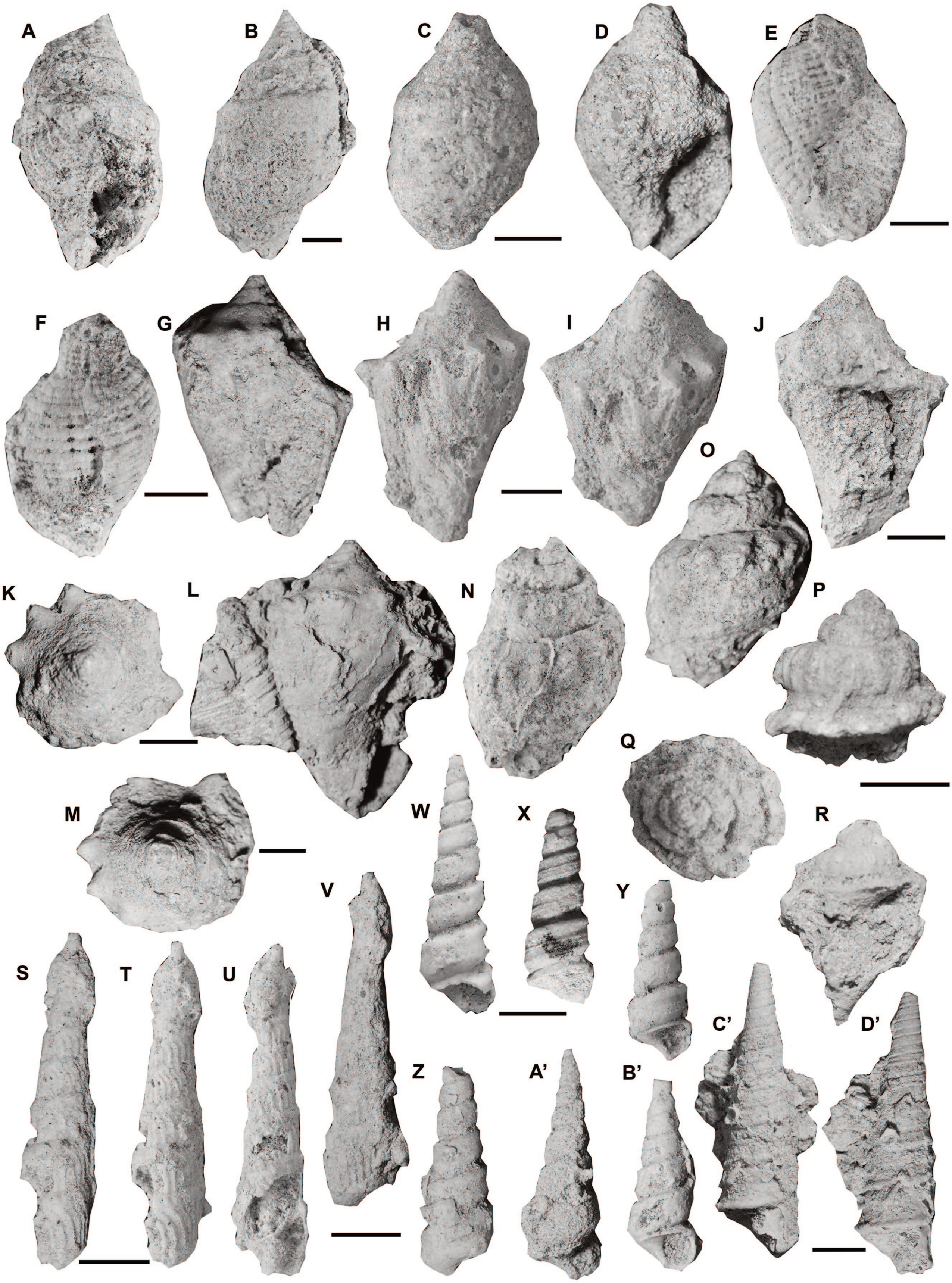
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. The fossil species of the Family Struthiolariidae from southern South America and Antarctica were extensively studied by several authors (Ihering, 1897, 1907; Ortmann, 1902; Marwick, 1924; Zinsmeister & Camacho, 1980; Camacho & Zinsmeister, 1989; López Cabrera & Olivero, 2021). Previous names used for members of this group were *Struthiolaria* (Ihering, 1897, 1907) and *Struthiolarella* (Steinmann & Wilckens, 1908; Zinsmeister & Camacho, 1980; Camacho & Zinsmeister, 1989), a new name proposed for grouping South American species. The nomenclatural status of this taxon was discussed by Powell (1951), Nielsen (2005), and López Cabrera & Olivero (2021), who considered *Struthiolarella* as a junior synonym of *Perissodonta* Martens, 1878.

Perissodonta is characterized by having medium-sized shells with very variable outlines, frequently pyramidal to globose, with moderately elevated spire (shorter than last whorl), convex to squarish whorls, sculpture smooth or given by several spiral threads and/or cords, and axial elements in the peripheral line of sutural ramp (Zinsmeister & Camacho, 1980; Camacho & Zinsmeister, 1989). These features are present in our material. The related genus *Antarctodarwinella* Zinsmeister, 1976, lacks sculpture in the last whorl, a character present in our specimens.

Systematics of the family in South America are the object of some studies due to their high variability regarding shell outline and sculptural elements, with some authors considering a high number of species (Camacho & Zinsmeister, 1989; Genta Iturrería & Griffin, 2018) and others considering some of them as synonyms (López Cabrera & Olivero, 2021). One of the most variable species is *Perissodonta ameghinoi* (Ihering, 1897), which presents a scalariform outline, elongated axial elements, and well-developed spiral cords towards the anterior end and thin threads towards the suture. In particular, *P. ameghinoi* is distinguished by the number of axial elements per whorl

Figure 4. A–D, *Buccinanops halleri* sp. nov., CNP-PIIc 1412 (paratypes); A–B, apertural views; C–D, lateral views; E–F, *Miomelon gracilior* (Ihering, 1896), CNP-PIIc 1418; E, apertural view; F, lateral view; G–M, *Pachycymbiola camachoi* del Río and Martínez, 2006, CNP-PIIc 1420; G, J, L, apertural views; H–I, lateral views; K, M, apical views; N–R, *Perissodonta ameghinoi* (Ihering, 1897), CNP-PIIc 1426; N, lateral view; O, apertural view; P, R, spires in lateral view; Q, apical view; S–V, *Zeacuminia santacruzensis* (Ihering, 1897), CNP-PIIc 1429, lateral views; W–B', "*Turritella*" *ambulacrum* Sowerby, 1846, CNP-PIIc 1433; W, Y, A'–B', apertural views; X, Z, lateral views; C'–D', "*Torcula*" cf. "*T.*" *hauthali* Ihering, 1907, CNP-PIIc 1434, lateral views. Scale = 10 mm (H–D'), 5 mm (A–B, E–G), 2 mm (C–D).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(12 to 18) and the development of last spiral cords (4 to 7 more marked cords) (López Cabrera & Olivero, 2021). The morphologically close species *P. ornata* (Sowerby, 1846) differs in the number of axial elements (generally fewer ones) and in the presence of two or three stronger cords towards the suture in the last whorl (Camacho & Zinsmeister, 1989; López Cabrera & Olivero, 2021). The Bryn Gwyn specimens here analyzed are assigned to *P. ameghinoi*, considering their sculpture and number of axial elements.

Perissodonta ameghinoi is widely distributed, occurring in the Miocene of Chenque, Monte León, and Carmen Silva formations (Camacho & Zinsmeister, 1989; López Cabrera & Olivero, 2021) and the Oligocene to Miocene of Santo Domingo Formation (Chile) (Nielsen, 2005). The new record here extends the geographical and stratigraphical distribution of the species to the Gaiman Formation in the Chubut Province.

TEREBRIDAE Mörch, 1852

Genus ***Zeacuminia*** Finlay, 1930

Type species. *Zeacuminia tahuia* Finlay, 1930. Original designation. Eocene, New Zealand.

Zeacuminia santacruzensis (Ihering, 1897)
Figure 4S–V

Referred Material. CNP-PIIc 1429, three recrystallized and composite molds; diameter range: 7.1– 9.2 mm (mean= 8.23 mm), height range: 14.3–49.8 mm (mean= 31 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. The Terebridae are characterized by high shells with nearly straight sides and numerous whorls, and sculpture given by mainly axial elements. Sowerby (1846) recognized this group for the first time for Chilean Cenozoic sediments, represented by *Zeacuminia costellata* and *Terebra undulifera* (Griffin & Nielsen, 2008). Later, Ihering (1897) described two other Terebridae for the Early Miocene of Santa Cruz Province, today known as *Z. quemadensis* and *Z. santacruzensis*. The main difference between these two species is the presence of a subsutural groove in the second one, with axial ribs not reaching the apical suture (Ihering, 1897; Ortmann, 1902). This character is present in the specimens here reported from the Gaiman Formation.

Zeacuminia santracruzensis was previously known from the Monte León Formation (Ihering, 1897; del Río, 2004) in Santa Cruz. The present record extends its geographic distribution to the Chubut Province. Del Río (2004) proposes the first occurrence of this genus in Patagonia within the RSP Assemblage. Beu et al. (1997) considered the genus a "Cenozoic disperser" between New Zealand and South America.

TURRITELLIDAE Lóven, 1847

Remarks. The Family Turritellidae is one of the most abundant groups of gastropods in the Patagonian Cenozoic marine outcrops. It is considered an excellent marker for Cenozoic levels (see Allmon and Knight, 1993), although it is poorly represented in present molluscan assemblages of South America. Nevertheless, it has been mentioned in several stratigraphical and sedimentological studies of the Cenozoic (*e.g.*, Scasso and Castro, 1999; del Río et al., 2001; Casadío and Griffin, 2009; Palazzesi et al., 2021), or even it has been the target of taphonomic studies (*e.g.*, Kronemberger and Parras, 2024). However, Patagonian turritellids are severely neglected in systematics studies (Griffin and Nielsen, 2008). As a consequence, the taxonomic knowledge of the family in the Patagonian Cenozoic is poorly understood. Most of its taxa have been historically assigned to "*Turritella*" (*e.g.*, Ortmann, 1902; Ihering, 1907), presently considered a waste-basket taxon (see Plotnick and Wagner, 2006). During the last decades, other genera such as *Spirocolpus* or *Torcula*, have been mentioned (*e.g.*, del Río, 2004; Reichler, 2010) and in recent years new comprehensive studies have been carried out on Turritellidae taxonomy and systematics (*e.g.*, DeVries, 2007; Friend et al., 2023). However, more updated systematic studies about Turritellidae in the Patagonian Cenozoic deposits are required. The present research provides a preliminary approach to the classification of Turritellidae from the Gaiman Formation in the Chubut Province.

"***Turritella***" ***ambulacrum*** Sowerby, 1846
Figure 4W–4B'

Referred Material. CNP-PIIc 1431-1433, 43 recrystrallized, internal and composite molds; diameter range: 5.5–10.1 mm (mean= 8.4 mm), height range: 16.7–33.5 mm (mean= 25 mm).
Geographic and Stratigraphic Distribution. Fossiliferous levels 3, 4, 6, 7, and 8. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. "*Turritella*" *ambulacrum* and "*Turritella*" *patagonica* Sowerby, 1846 are the most abundant turritellid species in Early Miocene outcrops of the Patagonian Cenozoic (del Río, 2004; Griffin and Nielsen, 2008). The main differences between the two species regard the apical angle, suture, spiral cords, and aperture. The apical angle is more reduced in "*T.*" *ambulacrum*, with slightly convex to subquadrate whorls, suture deeply incised, more developed sutural ramps, less pronounced spiral cords, and a larger and more circular aperture. The specimens here studied fit with the morphological features of "*T.*" *ambulacrum*. Most of the studied material consists of internal and composite molds of different sizes, but several specimens present more detailed preservation that allows to confirm specific assignment.

Previously, Ihering (1904, 1907), Frenguelli (1935), and Feruglio (1949) mentioned "*Turritella*" *ambulacrum* for the Chubut River area. This species is also known in many other Early Miocene stratigraphic units, including the San Julián, Monte León, and Chenque formations (del Río, 2004).

"***Torcula***" cf. "***T.***" ***hauthali*** Ihering, 1907
Figure 4C'–D'

Referred Material. CNP-PIIc 1434, two specimens; diameter range: 13.8–15.1 (mean= 14.5 mm), height range: 45.2–51.4 mm (mean= 48.3 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Besides "*Turritella*" *ambulacrum* and "*T.*" *patagonica*, other turritellid species were present in the Early Miocene of Patagonia (Ortmann, 1902; Ihering, 1907). Among them, the genus *Torcula* was mentioned with doubts by del Río (2004) to include the species "*T.*" *hauthali* from Camarones and Pico Salamanca localities. This genus is characterized by the presence of large shells with concave whorls ornamented by two prominent spiral cords separated by a deep sulcus (Friend et al., 2023). "*Torcula*" *hauthali* presents an apical spiral cord stronger than a basal spiral cord (Ihering, 1907) but in our material, both spiral cords are equally developed. This could be due to the poor preservation of the specimens. Therefore, we decided to doubtfully assign our material to "*T.*" *hauthali*.

Ihering (1907) and Camacho and Fernandez (1956) mentioned the species "*T.*" *hauthali* from Camarones and Pico Salamanca localities in the Chenque Formation. In addition, Camacho and Fernandez (1956) indicated its presence in the Gaiman Formation, at the Dos Pozos locality.

AUSTROSIPHONIDAE Cotton and Godfrey, 1938

Genus ***Penion*** Fischer, 1884

Type species. *Fusus dilatata* Quoy and Gaimard, 1833 (= *Penion sulcatus*). Original designation. Recent, New Zealand.

Penion subrectus (Ihering, 1899)
Figure 5A–F

Referred Material. CNP-PIIc 1427-1428, five composite molds; diameter range: 13.1–27.5 mm (mean= 20.9 mm), height range: 26.2–50.1 mm (range= 34.9 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Fossil "whelk shells" (Superfamily Buccinoidea) were recognized in the Cenozoic of Patagonia by Sowerby (1846), and they were assigned to the genera *Buccinum*, *Cominella*, *Fusus*, *Siphonalia*, *Chrysodomus* and *Aeneator* (d'Orbigny, 1852; Philippi, 1887; Ihering, 1899, 1907; Ortmann, 1902; del Río, 2004). Ponder (1973) placed several South American species of whelk shells in the genus *Penion*: *P. subreflexus* (Sowerby, 1846), *P. domeykoanus* (Philippi, 1887), and *P. subrectus* (Ihering, 1899), from Chile and Argentina. Later works revised and discussed the systematic status of these species and proposed new ones (Frassinetti, 2001, 2006; Nielsen, 2003; Griffin & Nielsen, 2008; Reichler, 2010).

Penion subrectus is the most common species in the Patagonian Cenozoic sediments (del Río, 2004), and is characterized by having a biconical fusiform shell with convex whorls, broad and inclined shoulders, elevated spire (generally near to one third to a half of total height), last whorl with 10–11 axial enlarged nodules or knobs crossing shoulders, nearly straight siphonal channel, and sculpture given by several thin spiral cords. Specimens of the Gaiman Formation share all of these characters, allowing us to assign them to *P. subrectus*. The only other *Penion* species recognized in Patagonia is *P. patagoniensis* Reichler, 2010, is characterized by broader and more developed shoulders and a more elevated spire than *P. subrectus*. Chilean species, such as *P. darwinianus* (Philippi, 1887), have more elongated spires.

Penion subrectus is recognized in other Patagonian stratigraphic units: San Julián, Monte León, and Chenque formations (Ihering, 1907; del Río et al., 2022a). Also, *Penion patagoniensis* Reichler, 2010, occurs in the coeval Gran Bajo del Gualicho Formation (Reichler, 2010). Beu et al. (1997) proposed a New Zealand origin for the species-group among which *P. subrectus* is included, with posterior dispersal both to and from New Zealand-Australia and South America.

TUDICLIDAE Cossmann, 1901

Genus ***Aeneator*** Finlay, 1926

Type species. *Verconella marshalli* Murdoch, 1924 (=*Aeneator marshalli*). Original designation. Recent, New Zealand.

Aeneator annae (Ortmann, 1900)
Figure 5G–J

Referred Material. CNP-PIIc 1430, two composite molds; diameter range: 7.6–9.4 mm (mean= 8.5 mm), height range: 14.8–18.3 mm (mean= 16.6 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Another “whelk shell” recognizable among the gastropods recovered from the Gaiman Formation is *Aeneator annae*. This species is characterized by having a fusiform shell with elongated-oval outline, high spire, approximately 7–8 whorls with axial elements, last whorl large with 12–14 axial elements, crossed by slightly spiral threads, aperture elongated and ovate, and a short-reflexed canal. The material of the Gaiman Formation consists of only two poorly preserved specimens with small-sized shells for the species.

Ortmann (1900) assigned this species to the genus *Cominella* Gray, 1850, but posteriorly, del Río (2004) named it as *Aeneator*? *annae*. Further taxonomic studies of the Cenozoic “whelk shells” of Patagonia are required.

Previously, *A. annae* has been recovered from the Monte León Formation (Ortmann, 1902) and is part of the RSP assemblage of del Río (2004).

BIVALVIA Linnaeus, 1758
GLYCYMERIDIDAE Dall, 1908

Genus ***Glycymerita*** Finlay and Marwick, 1937

Type species. *Glycymeris concava* Marshall, 1917 (=*Glycymerita concava*). Original designation. Early Paleocene, Wangaloa Formation, New Zealand.

Glycymerita camaronesia (Ihering, 1907)
Figure 5K–M

Referred Material. CNP-PIIc 1444, ten composite molds; height range: 85.3–97.2 mm (mean= 90.9 mm), length range: 81.1–106.4 mm (mean= 95.85 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Glycymeridids shells are frequently found in the upper fossiliferous level of the Bryn Gwyn section. They have subquadrate outlines, strong inflation, and presence of flat-topped radial ribs. These characters allow us to consider them as representatives of the genus *Glycymerita*. In addition, the presence of more subquadrate instead subcircular outline, prominent umbos, strong hinge teeth that become horizontal towards the ends, and clearly developed middle teeth allow to assign the specimens to the species *G. camaronesia* (del Río and Camacho, 1998). Another Early Miocene *Glycymerita* species is *G. cuevensis* (Ihering, 1897), a species characterized by a more sub-

circular outlined shell, less prominent umbos and poorly developed middle teeth than *G. camaronesia*.

Frenguelli (1935) mentioned the occurrence of the glycymeridid "*Pectunculus*" *cuevensis* (Ihering, 1897) in this area, probably based on specimens of the taxon here studied.

The species *G. camaronesia* is known from the Chenque Formation in southern Chubut Province. Other species of the family Glycimerididae are also present in the Early Miocene Monte León Formation and in the Late Miocene Puerto Madryn Formation (del Río 1992, 2004; del Río and Camacho, 1998).

OSTREIDAE Rafinesque, 1815

Genus ***Crassostrea*** Sacco, 1897

Type species. *Ostrea virginica* Gmelin, 1791 (=*C. virginica*). Original designation. Recent, North Atlantic Ocean, North America, and Europe.

Crassostrea*? *hatcheri (Ortmann, 1897)
Figure 5N–R

Referred Material. MPEF-PI 1393–1394, 1396, 1398, four specimens; height range: 157.9–187.2 mm (mean= 174.7 mm), length range: 154–167 mm (mean= 161.2 mm).

Geographic and Stratigraphic Distribution. Fossiliferous levels 1, 2, 6, and 8. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Large oyster shell concentrations are a hallmark of Neogene sediments in Patagonia (*e.g.*, Parras and Casadío, 2006). Their presence first noted in geological and paleontological studies of the Upper Valley of Chubut River. Since Ihering (1907), several posterior authors mentioned the occurrence of large oyster shells, named as *Ostrea patagonica* d'Orbigny, 1839 (Ihering, 1907; Frenguelli, 1935); *Ostrea hatcheri* (Frenguelli, 1927, 1935, Simpson, 1935; Haller and Mendía, 1980); *Ostrea maxima* Hupé, 1854 (Camacho and Fernandez, 1956; Haller and Mendía, 1980); *Ostrea* (Scasso and Castro, 1999), or simply "oysters" (Scasso and Bellosi, 2004; Cuitiño et al., 2019). There is consensus in the determination of two species of large oysters for the Miocene of Chubut: *Crassostrea*? *hatcheri* in the Early Miocene, and "*Ostrea*" *patagonica* in the Late Miocene (Cabrera, 1928; Brito, 2009). The two species are often found mixed because of the high resistance of shells to erosion when they are free of sediment. *Crassostrea*? *hatcheri* is characterized by a deep, subrectangular and broad ligamental groove, external sculpture including numerous lamellae and often some radial ondulations near to the ventral margin, and without inner crenulations (Saporiti, 1938; Parras and Casadío, 2006). Oysters *in situ* from the levels of the Gaiman Formation in the Bryn Gwyn area correspond to this species. They are found forming small clusters or alone.

Crassostrea? *hatcheri* is known from several Early Miocene stratigraphic units, including San Julián, Monte León, Chenque, Estancia 25 de Mayo, and Gran Bajo del Gualicho formations (Saporiti, 1938; Parras and Casadío, 2006).

PLICATULIDAE Gray, 1854

Genus ***Plicatula*** Lamarck, 1801

Type species. *Spondylus plicatus* Linnaeus, 1764 (=*P. plicata*). Original designation. Recent, Indopacific Ocean, Eastern Africa coast.

Plicatula sp.
Figure 5S–U

Referred Material. CNP-PIIc 1452, a right valve (height= 20.3 mm, length= 25.1 mm).

Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Plicatulids are a group of bivalves with a wide stratigraphic range (from the Middle Triassic to Recent), represented in the Cenozoic by a single genus, *Plicatula*. It is known in Patagonia from the Paleocene (del Río et al., 2011), but there are no other records until Pleistocene times (Aguirre and Farinati, 2000).

Only one right valve was found in the Bryn Gwyn section, which is small-sized, inequilateral and irregular in outline, very curved, with cardinal area very small with triangular resilifer and two straight crurae, external sculpture given by ten large plicae, which are more pronounced towards the margin. This shell resembles the species *P. gibbosa* Lamarck, 1801, living in the Western Atlantic Ocean (Dall, 1925).

CARDITIDAE Férussac, 1822

Genus ***Neovenericor*** Rossi de García, Levy and Franchi, 1980

Type species. *Venericor* (*Venericor*) *abasolensis* Camacho and Fernandez, 1956 (=*N. austroplata* Gardner and Bowles 1939). Original designation. Early Miocene, Chenque Formation, Argentina.

Neovenericor camachoi Pérez, Cuitiño and Soto, 2025
Figure 5V–W

Referred Material. CNP-PIIc 1141 (holotype), CNP-PIIc 1142 (paratypes), CNP-PIIc 1143-1146, 1417, 1421-1422, 81 recryztallized valves, internal, external and composite molds; height range: 28.3–121.7 mm (mean= 55.33 mm), length range: 29.8–127 mm (mean= 55.6 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. The presence of "planicostate" carditid bivalves in the Gaiman Formation was first noticed by Camacho and Fernandez (1956). Later, Haller and Mendía (1980) and Scasso and Castro (1999) mentioned the presence of carditids. This finding was one of the arguments for the Eocene age proposed for this stratigraphic unit, and was discussed by subsequent authors (Camacho, 1974, 1981; Rossi de García et al., 1980; del Río, 2004; Reichler, 2011; among others). The generic placement of these "planicostate" carditids was discussed in these works, some placing them in the Northern Hemisphere genus *Venericor* and others in the South American genus *Neovenericor*. Pérez et al. (2017), based on a morphometric approach, confirmed the assignment to *Neovenericor*. A most recent study carried out by Pérez et al. (2025) erected the new species *N. camachoi* for specimens collected in the Gaiman Formation at Bryn Gwyn and Cañadón del Puma localities. This is the specific assignment followed here.

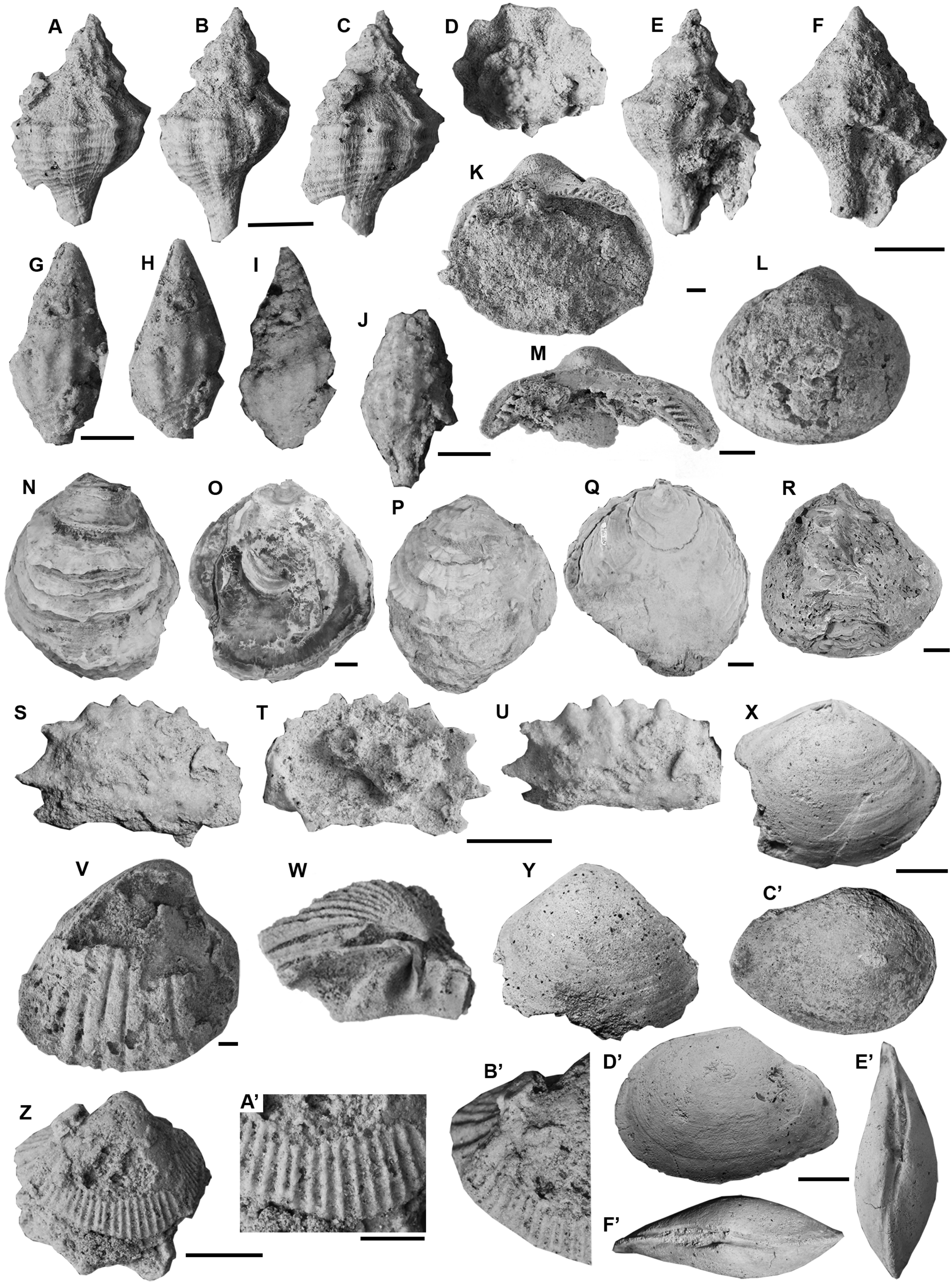
The genus *Neovenericor* is also found in the Chenque Formation in southern Chubut Province, and in the Gran Bajo del Gualicho (Saladar Member), Vaca Mahuida, and Río Foyel formations in Río Negro Province, the Paraná Formation in Entre Ríos Province, and the Río Turbio Formation in Santa Cruz Province (Pérez et al. 2017, 2025). The Chenque, Gran Bajo del Gualicho (Saladar Member), and Vaca Mahuida formations are partially correlated to the Gaiman Formation (Bellosi and Barreda, 1993; Reichler, 2011; Cuitiño et al., 2015a; Parras and Cuitiño, 2021). The *Neovenericor* species found in the coeval Chenque and Gran Bajo del Gualicho formations is *N. austroplata*, a species very closely related to *N. camachoi* (Pérez et al., 2025).

CRASSATELLIDAE Férussac, 1822

Crassatellidae gen. et sp. indet.
Figure 5X–Y

Referred Material. CNP-PIIc 1435 two composite molds; height range: 21.5–31.3 mm (mean: 26.4 mm), length range: 28.8–37.5 mm (range: 33.2 mm), incomplete specimens.
Geographic and Stratigraphic Distribution. Fossiliferous levels 6 and 8. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Specimens here assigned to the family Crassatellidae consist of composite molds preserving articulated valves of small size. Valves have a subtriangular

Figure 5. A–F, *Penion subrectus* (Ihering, 1899), CNP-PIIc 1428; A–C, lateral views; D, apical view; E, apertural view; F, CNP-PIIc 1427, apertural view; G–J, *Aeneator annae* (Ortmann, 1900), CNP-PIIc 1430, lateral views; K–M, *Glycymerita camaronesia* (Ihering, 1907), CNP-PIIc 1444; K, interior view of the right valve; L, external view of the right valve; M, left hinge; N–R, *Crassostrea*? *hatcheri* (Ortmann, 1897); N–O, MPEF-PI 1393; N, external view of the left valve; O, internal view of the left valve; P–Q, MPEF-PI 1398; P, external view of the left valve; Q, external view of the right valve; R, MPEF-PI 1394, external view of the left valve; S–U, *Plicatula* sp., CNP-PIIc 1452; S, external view of the right valve; T, internal view of the right valve: U, lateral view of the right valve; V–W, *Neovenericor camachoi* Pérez, Cuitiño and Soto, 2025; V, CNP-PIIc 1141 (holotype), external view of the right valve; W, CNP-PIIc 1142 (paratype), left hinge; X–Y; Crassatellidae gen. et sp. indet.; X, external view of the left valve; Y, external view of the left valve; Z–B', *Patagonicardium philippi*? (Ihering, 1897), CNP-PIIc 1436; Z, external view of the left valve; A', close-up of the external sculpture; B', close-up of the anterior end; C'–E', *Macoma perplana* (Ihering. 1897), CNP-PIIc 1437; C', external view of the right valve; D', external view of the left valve; E', dorsal view; F', ventral view. Scale = 20 mm (N–R), 10 mm (A–F, K–M, S–Z, C'–F'), 5 mm (G–J, A'–B').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outline and they are enlarged in the antero-posterior axis, with a projected posterior portion. Umbones are convex and rounded. Very thin commarginal lines cover the valves. The presence of a conspicuous escutcheon and a hinge with a large and triangular middle tooth in a visible hinge allows assigning them to the family Crassatellidae. Some genera of the family are known from the Cenozoic of Argentina, such as *Crassatella* s. s., *Bathytormus*, *Spissatella*, and *Talabrica* (Santelli and del Río, 2014). General outline and sculpture of the Gaiman Formation specimens are similar to those of *Crassatella* s. s., but the incompleteness of the material precludes a more precise assignation.

Crassatellidae are found in the Early Miocene Monte León Formation and in the Late Miocene Puerto Madryn Formation (Santelli and del Río, 2014). A previous mention of the family in the Gaiman Formation was made by Camacho and Fernandez (1956). These authors mentioned the presence of *Crassatellites* sp. in the locality of Estancia Tolosa.

CARDIIDAE Lamarck, 1809

Genus ***Patagonicardium*** Frassinetti and Covacevich, 1999

Type species. *Cardium philippi* Ihering, 1897 (=*Patagonicardium philippi*). Original designation. Miocene, Argentina and Chile.

Patagonicardium philippi? (Ihering, 1897)
Figure 5Z–B′

Referred Material. CNP-PIIc 1436, two incomplete internal molds; height range: 19.6–23.2 (mean= 21.4 mm), length range: 24.7–27.3 mm (mean= 26 mm).
Geographic and Stratigraphic Distribution. Fossiliferous levels 6 and 8. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Cardiid specimens from the Gaiman Formation are probably juvenile and poorly preserved, but some characters can be observed. These cardiids have inflated shells with subcircular outline, prominent and rounded umbos, numerous radial ribs with subtriangular section, and a marked lunule. Also, differences in radial ribs can be observed: posterior ribs are narrower than the middle ones, and anterior ribs are wider than the others. These characters are present in the South American species *Patagonicardium philippi*, but the absence of hinge features prevents providing a more precise assignment.

Patagonicardium philippi is also mentioned in the literature as *Hedecardium* (*Iheringicardium*) *phillippi*, a name proposed by Schneider (2002). The name *Patagonicardium* was indicated by Frassinetti and Covacevich (1999), prior to the mentioned proposal of Schneider. The latter author was apparently not aware of the existence of the previous name, and because of this, the name *Iheringicardium* becomes a junior synonym of *Patagonicardium*.

The species *P. philippi* is one of the most abundant cardiids found in the Early Miocene of southern South America; it is also recognized also in the Monte León and Guadal (Chile) formations (Frassinetti & Covacevich, 1999; del Río, 2021).

TELLINIDAE Blainville, 1814

Genus ***Macoma*** Leach, 1819

Type species. *Tellina tenera* Leach, 1819—*Macoma calcarea* (Gmelin, 1791). Original designation. Recent, Arctic Sea.

Macoma perplana (Ihering, 1897)
Figure 5C′–E′

Referred Material. CNP-PIIc 1437, five internal molds; height range: 25.1–35.2 mm (mean: 29.7 mm), length range: 34.4–49.4 mm (mean: 40.4 mm).
Geographic and Stratigraphic Distribution. Fossiliferous levels 6, 7, and 8. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. *Macoma perplana* is one of the most abundant bivalves in the Gaiman Formation at Bryn Gwyn locality. Representatives of the species are always preserved as complete and articulated internal molds. Diagnostic characters for species identification included a shell morphology with a suboval outline, small umbones positioned near the middle of the dorsal margin, an acute and truncated posterior margin with a curvature in dorsal view, and right valves that are slightly larger than left ones (Ihering, 1897). All of these characters are present in our

specimens, and differ from other fossil Tellinidae of Patagonia mainly in size and outline and morphology of the posterior margin.

Macoma perplana was one of the first bivalve species recognized in the Lower Valley of the Chubut River area (Frenguelli, 1927, 1935) (as *Sanguinolaria perplana*). The species is also found in the Miocene Monte León and Puerto Madryn formations (Ihering, 1897; del Río & Martínez, 1998).

VENERIDAE Rafinesque, 1815

Genus ***Ameghinomya*** Ihering, 1907

Type species. *Venus volckmanni* var. *argentina* Ihering, 1897 (=*Ameghinomya argentina*). Original designation. Miocene, Argentina and Chile.

Ameghinomya argentina (Ihering, 1897)
Figure 6A–D

Referred Material. CNP-PIIc 1438 and 1439, six molds; height range: 48.7–66.8 mm (mean= 55.1 mm), length range: 53.8–67.1 mm (mean= 58.3 mm).
Geographic and Stratigraphic Distribution. Fossiliferous levels 2, 3, 6, and 8. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. The presence of venerid bivalves is frequent in the Gaiman Formation as small internal molds (Cuitiño et al., 2019). There are two previous mentions of venerid bivalves for the unit: *Chione patagonica* (Philippi, 1887) and *Chione argentina* (Ihering, 1897) (Ihering, 1907; Frenguelli, 1935). Probably, these last two mentions correspond to a single taxon, here recognized as *Ameghinomya argentina*. The Gaiman specimens have large and circular to subcircular shells, with straight dorsal margin, nearly flat lunule, poorly defined escutcheon, external sculpture given by low lamellar commarginal ribs with fine numerous radial ribs, and very fine crenulations in the inner ventral margin, all characters present in *Ameghinomya argentina* according to the description of Pérez et al. (2013).

Specimens are preserved as internal, external, or composite molds in the fossiliferous levels 1, 3, and 7, with a wide range of sizes, representing closed or individual shells. In contrast, in the fossiliferous level 8, specimens are always found as large, closed shells preserved as consolidated composite molds.

Ameghinomya argentina is a widespread taxon, already known from the Early Miocene Monte León and Chenque formations, the Saladar Member of the Gran Bajo del Gualicho Formation (Early Miocene), and the Late Miocene Puerto Madryn and Paraná formations.

Genus ***Austrocallista*** Erdmann and Morra, 1985

Type species. *Meretrix iheringi* Cossmann, 1898 (= *Austrocallista iheringi*). Original designation. Late Oligocene to Early Miocene, San Julián, Monte León, El Chacay, and Carmen Silva formations, Argentina.

Austrocallista iheringi (Cossmann, 1898)
Figure 6E–I

Referred Material. CNP-PIIc 1440, 1441, and 1443, 17 composite molds; height range: 35.1–48.6 mm (mean= 40.35 mm), length range: 38.1–51.4 mm (mean= 45.2 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Among the venerid shells recognized in Bryn Gwyn, several specimens can be assigned to *Austrocallista iheringi*, based on the presence of medium to large shells, with subtriangular to suboval outline with a thin and well-developed dorsoposterior carina, lunule long and convex, escutcheon very narrow to absent, nymphs sculptured by very faint vertical ribs, socket for a large anterior lateral hinge tooth in the right valve, narrow inner ventral margin, and sculptured by regular commarginal lines with rounded section. The description of *A. iheringi* follows Alvarez et al. (2020). Another venerid genus with sculptured nymph is *Eucallista*, which differs from *Austrocallista* in the presence of deeper lunule and the presence of escutcheon (Alvarez et al., 2020).

Austrocallista iheringi is a well-known and widespread taxon in the Early Miocene of Patagonia, with presence in the Monte León, El Chacay, and Carmen Silva formations (Alvarez et al., 2020). Here we report the first record of the species from the Gaiman Formation in the Chubut Province, expanding its geographic range.

Genus ***Retrotapes*** del Río, 1997

Type species. *Retrotapes ninfasiensis* del Río, 1997. Original designation. Late Miocene, Puerto Madryn Formation, Argentina.

Retrotapes ninfasiensis del Río, 1997
Figure 6J–K

Referred Material. CNP-PIIc 1442, three composite molds; height: 55.8 mm, length: 63.4 mm, one complete specimen.
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. *Retrotapes* is a geographically and stratigraphically widespread venerid genus, with fossil records from the Eocene to Recent in Antarctica, Tierra del Fuego, Santa Cruz, Chubut, and Southern Chile, and living records in the Eastern Pacific and Western Atlantic oceans, from Perú to Rio Grande do Sul (Brazil). The Miocene record of the genus comes from Carmen Silva, Monte León, and Puerto Madryn formations in Argentina; the Navidad and Guadal formations in Chile, and McMurdo Sound in Antarctica (Alvarez, 2019).

The specimens from the Bryn Gwyn locality have subquadrate and slightly convex shells and a large, deep and concave lunule. These characters match with the genus and its type species, *R. ninfasiensis*, previously known from the Late Miocene of the Puerto Madryn Formation (del Río, 1997; Alvarez, 2019). Other species of *Retrotapes*, such as *R. striatolamellata* (Ihering, 1897) and *R. fuegoensis* (del Río, 1997) have more inflated, rounded in outline, and longer shells than *R. ninfasiensis*.

This record expands the stratigraphic span of the species *R. ninfasiensis* to the Early Miocene.

PHOLADIDAE Lamarck, 1809

Genus ***Cyrtopleura*** Tryon, 1862

Type species. *Pholas cruciger* Sowerby, 1834 (=*C. crucigera*). Subsequent designation (Stoliczka, 1871). Recent, North Atlantic Ocean.

Cyrtopleura lanceolata (d'Orbigny, 1841)
Figure 6L–M

Referred Material. CNP-PIIc 1454, a composite mold, height: 13.8 mm, length: 30.2 mm.
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. The Pholadidae is a group of sediment-dwelling bivalves with a broad fossil record mainly given by traces (*e.g.*, *Gastrochaenolites*, see Carmona et al., 2007). Occasionally, valves or molds are preserved allowing for more precise taxonomic determination. In this specimen, the presence of an elongated shell of small size, with minute beaks placed near the anterior margin, which is truncated, the absence of anterior-ventral callus and umbonal-ventral groove allows us to assign the specimen here reported to *Cyrtopleura lanceolata*. Other pholadids known from the Cenozoic of Patagonia, such as the genera *Barnea* or *Pholadidea*, present a conspicuous callus, not recognized in our specimen.

Previously, Ihering (1907) mentioned the occurrence of *Martesia patagonica* (Philippi, 1887) in the area, but *Martesia* presents a callus, and this character is not recognized in *Cyrtopleura*. The species *C. lanceolata* was recorded in the Late Miocene Puerto Madryn, Paraná, and Camacho formations (del Río & Martínez, 1998).

SCAPHOPODA Bronn, 1862
DENTALIIDAE Children, 1834

Genus ***Fissidentalium*** Fischer, 1885

Type species. *Dentalium ergasticum* Fischer, 1883—*F. capillosum* (Jeffreys, 1877). Original designation. Recent, North Atlantic Ocean.

Fissidentalium? sp.
Figure 6R

Referred Material. CNP-PIIc 1445, an incomplete shell preserved as external mold (length= 35.35 mm).
Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).
Remarks. Scaphopods are usually a minor group in marine Cenozoic fossil assemblages. We found only one incomplete external mold of a shell preserving external sculpture. The shell is conical, softly tapering towards the superior apex, sculptured by strong longitudinal and sharp ribs (at least seven preserved) with thick cross section, small secondary

ribblets between ribs, and gentle, pronounced annular growth lines. These characters are present in several species of the genus *Fissidentalium*, for example, living *F. zelandicum* (Sowerby, 1860) or *F. majus* (Sowerby, 1846) from New Zealand and Chile, respectively. Despite this, the absence of the superior apex of the shell precludes confirming the generic assignment.

The specimen here reported is the first scaphopod mentioned for the Gaiman Formation.

ECHINODERMATA Klein, 1778
ECHINOIDEA Schumacher, 1817
MONOPHORASTERIDAE Lahille, 1896

Genus ***Amplaster*** Martínez, 1984

Type species. *Amplaster coloniensis* Martínez, 1984. Original designation. Late Miocene, Uruguay.

Amplaster alatus Rossi de García and Levy, 1989
Figure 6N–P

Referred Material. CNP-PIIc 1446 and 1447, 19 incomplete tests and fragments; length: 42.9 mm, width: 53.3 mm of the most complete specimen.

Geographic and Stratigraphic Distribution. Fossiliferous levels 5 and 6. Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Irregular echinoids have been recognized in the Cenozoic outcrops of Patagonia for a long time (Desor, 1847; Ortmann, 1902). For the Early Miocene of the Upper Valley of the Chubut River, Scasso and Castro (1999) and Cuitiño et al. (2019) mentioned the presence of "echinoids" and "irregular echinoids". The species *Monophoraster darwini* was mentioned by Ihering (1904, 1907), and by del Río et al. (2021) in the Gaiman and Trelew areas. In outcrops assigned to the Gaiman Formation at the adjacent Isla Escondida area, Rossi de García and Levy (1989) described the species *Amplaster alatus*.

Specimens of irregular echinoids recovered in the Bryn Gwyn area consist of incomplete or fragments of tests, preserving lunule and periproct in some cases. All these specimens show a large and rounded lunule with a closely placed anus, and petaloids occupying a reduced portion of the test. Reconstructed outlines from various specimens indicate a strong alated shape. All these characters correspond to *Amplaster alatus*, the species previously described for the Isla Escondida levels (Rossi de García & Levy, 1989).

SCHIZASTERIDAE Lambert, 1905

Genus ***Brisaster*** Gray, 1855

Type species. *Brissus fragilis* Düben and Koren, 1846. Original designation. Recent, North Sea.

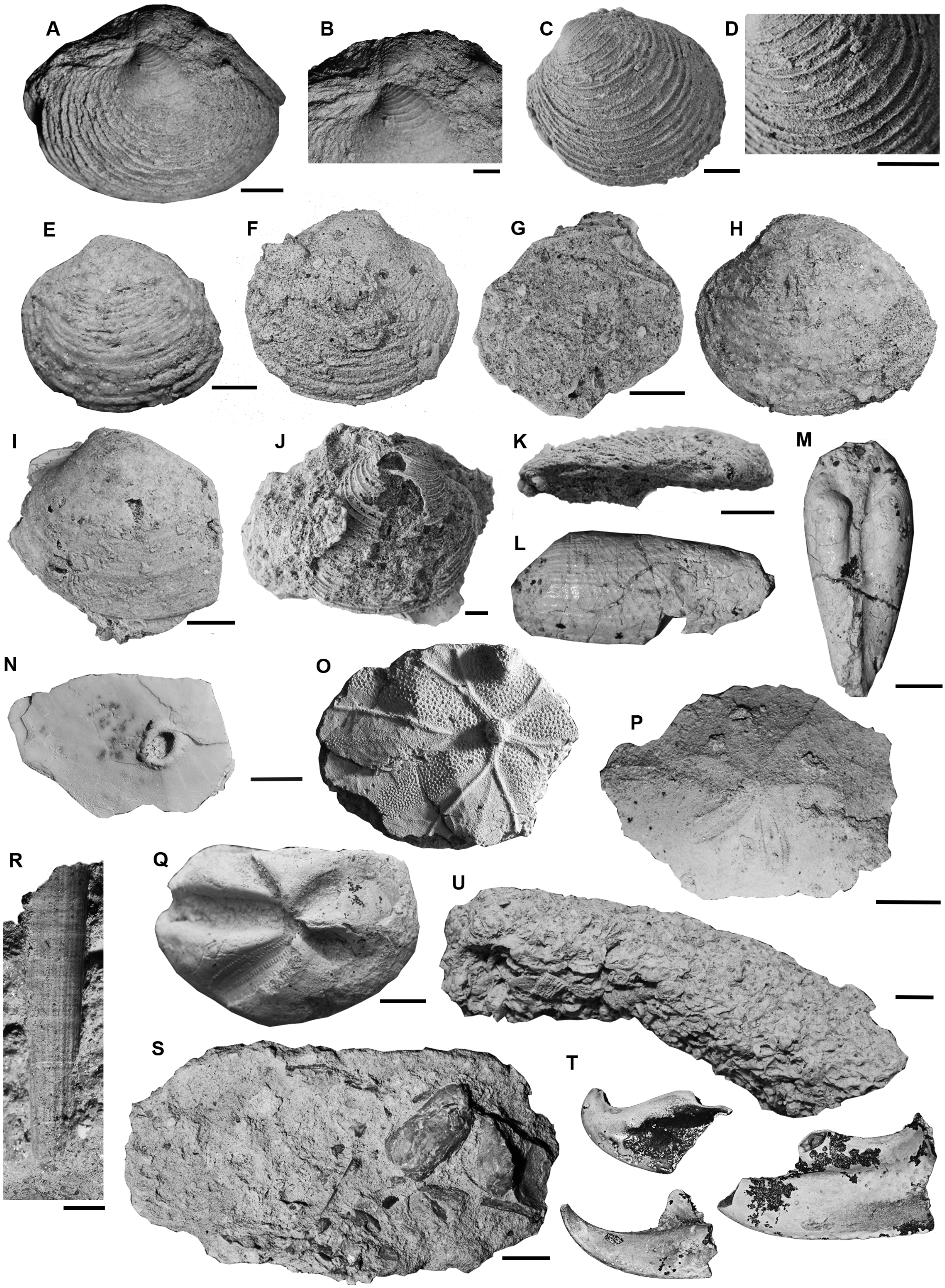
Brisaster iheringi (de Loriol, 1902)
Figure 6Q

Referred Material. CNP-PIIc 1448 and 1449, two tests; height range: 22.2–26.9 mm (mean= 24.6 mm), length range: 41.7–48.9 mm (mean= 45.3 mm).

Geographic and Stratigraphic Distribution. Fossiliferous level 5, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Beyond sand dollars, other irregular echinoids of Patagonian Miocene have been poorly studied (Martínez & del Río, 2017). Parma (2012) indicated the occurrence of the heart urchin genera *Brissopsis* and *Brisaster* from the Early Miocene of Patagonia in the Chenque and Carmen Silva

Figure 6. A–D, *Ameghinomya argentina* (Ihering, 1897); A, CNP-PIIc 1438, umbonal view of the left valve; B, close-up of umbonal external sculpture; C, external view of the left valve; D, close-up of the external sculpture; E–I, *Austrocallista iheringi* (Cossmann, 1898), CNP-PIIc 1440; E, external view of left valve; F, external view of right valve; G; internal view of the right valve; H, external view of the right valve; I, external view of right valve; J–K, *Retrotapes ninfasiensis* del Río, 1997, CNP-PIIc 1442; J, external view of the right valve; K, anterior view of the right valve with lunule; L–M, *Cyrtopleura lanceolata* (d'Orbigny, 1841), CNP-PIIc 1454; L, external view of the right valve; M, dorsal view; N–P, *Amplaster alatus* Rossi de García and Levy, 1989, CNP-PIIc 1446; N, close-up of lunule; O; detail of oral view; P; aboral view; Q, *Brisaster iheringi* (de Loriol, 1902), CNP-PIIc 1448, aboral view; R, *Fissidentalium*? sp., CNP-PIIc 1445, external mold; S–T, *Callianasa* sp., CNP-PIIc 1451; S, concretions including a partial cheliped and isolated fragments; T, isolated movable and fixed fingers; U, fragment of a bioturbation trace showing sparse specimens. Scale = 10 mm (A, C–L, N–P, Q–U), 5 mm (M, R), 3 mm (B).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formations. Additionally, Martínez and del Río (2017) added information about the presence of *Brisaster iheringi* in the Chenque Formation.

Heart urchin specimens from the Bryn Gwyn region are scarce, frequently preserved as composite molds. They have cordiform tests with the maximum width at the middle, the sulcus indenting the anterior margin, and the posterior margin truncated and inclined towards the apex. In aboral view, the posterior margin is straight. All of these characters are present in the species *Brisaster iheringi*, according to Martínez and del Río (2017).

The heart urchin *B. iheringi* is known from the Early Miocene Chenque and El Chacay formations (Martínez & del Río, 2017).

ARTHROPODA Gravenhorst, 1843
DECAPODA Latreille, 1802
CALLIANASSIDAE Dana, 1852
Genus ***Callianassa*** Leach, 1814

Type species. *Cancer* (*Astacus*) *subterraneus* Montagu, 1808 (=*C. subterranea*). Original designation. Recent, Atlantic Ocean, Caribbean Sea, and Mediterranean Sea.

Callianassa sp.
Figure 6S–T

Referred Material. CNP-PIIc 1450 and 1451, six concretions including isolated fragments and a partial first cheliped (carpus and merus), an isolated carpus, and eight isolated movable fingers and fixed fingers; carpus length range: 32.24–47.3 mm (mean= 37.9 mm).

Geographic and Stratigraphic Distribution. Fossiliferous level 6, Bryn Gwyn, Gaiman Formation, Early Miocene (Fig. 2).

Remarks. Crab remains were mentioned for the Bryn Gwyn section by Simpson (1935), and Haller and Mendía (1980). Later, Scasso and Castro (1999) recognized the presence of *Callianassa* sp. associated with *Ophiomorpha* burrows. We found numerous crab specimens in the studied section, including isolated fragments, carpus, merus, and fingers. All of these remains are here attributed to the genus *Callianassa*. This taxon was studied by Aguirre-Urreta (1990) for the adjacent locality of Estancia Tolosa. The author described the carpus as laterally compressed with a subquadrate outline in lateral view, a serrated upper border, and a smooth surface. *Callianassa* is a very speciose genus with more than a hundred, frequently poorly defined species. A more precise determination is unlikely to be possible based on these materials.

Callianassid remains and callianassid bioturbation (*Ophiomorpha*) are frequently associated in the area. Recurrently, callianassid remains are preserved within these burrows that form spoon-shaped phosphatic concretions (Scasso & Castro, 1999).

TAPHONOMY AND PRESERVATION

We acknowledge that rigorous field and laboratory observations of the taphonomic modifications will be required to obtain a robust dataset and thereby detect preservational trends across the fossiliferous levels. Nevertheless, in this section, we provide a general overview aimed to outline the taphonomic signature of the fossil invertebrates of the Gaiman Formation at Bryn Gwyn.

Most of the fossiliferous levels record consists of bioturbated muddy sandstones and fine sandstones with sparse specimens (*e.g.*, Fig. 6U), usually preserved as molds (*e.g.*, Fig. 5X, Y). Some levels with large, articulated oysters (*C.*? *hatcheri*) show higher fossil concentrations at about 30 m from the base of the section. A single, few centimeters-thick level (level 6) showing a sharp base and abundant reworked shell material represents 84% of the sample analyzed in this study, and comprises most of the invertebrate fossil diversity (93%) of the Gaiman Formation at Bryn Gwyn.

The examined materials display a wide spectrum of preservational styles, often reflecting both original skeletal features and subsequent diagenetic overprinting. Gastropod specimens, including "*Turritella*" *ambulacrum* (N=21; CNP-PIIc 1431; Fig. 4W–B') and *Zeacuminia santacruzensis* (N=5; CNP-PIIc 1429; Fig. 4S–V), are commonly recrystallized and sediment-filled, with low to moderate degrees of fragmentation and low degrees of encrustation (serpulids) and bioerosion (*Entobia* isp.). In contrast, *Pachycymbiola camachoi* (N=1; CNP-PIIc 1419; Fig. 4L) is represented by a relatively complete mold, showing no encrustation nor bioerosion and a low degree of abrasion on the external ornamentation. This specimen is associated with well-preserved bryozoan colonies (CNP-PIIc 1408; Fig. 3C–E) in densely packed bioclastic sands.

Among bivalves, individuals of *Neovenericor camachoi* (N=6; CNP-PIIc 1141, 1422; Fig. 5V, W) and *Retrotapes ninfasiensis* (N=3; CNP-PIIc 1442; Fig. 6J) are preserved as fragmented and recrystallized valves and molds, and in some cases with serpulid encrustations and a moderate degree of bioerosion (*Entobia* isp. and *Gastrochaenolites* isp.). In contrast, specimens of *Macoma perplana* (N=7; CNP-PIIc 1437; Fig. 5C'–E') occur as well-preserved articulated molds with minimal damage, whereas *Crassatellidae* indet. (N=3; CNP-PIIc 1435) shows fragmented molds with exceptional hinge details (Fig. 5X).

Regarding echinoids, remains of *Amplaster alatus* (N=17; CNP-PIIc 1446; Fig. 6N–P) occur as highly fragmented tests and molds. Some individuals preserved as molds retain three-dimensional details of delicate structures such as food grooves, peristome, and pores as positive relief (Fig. 6O). Moreover, an isolated individual of *Brisaster iheringi* (N=1; CNP-PIIc 1448) preserved as a mold with a low degree of fragmentation and no bioerosion or encrustation, preserves 3D morphology details (Fig. 6Q).

Concerning decapods, highly fragmented individuals (carpus and fingers) of *Callianassa* sp. (N=12; CNP-PIIc 1450) occur in reworked phosphatic concretions, with possibly original or slightly modified cuticular composition preserved and no bioerosion nor encrustation. The chelae (merus, carpus, propodus, isolated and fixed fingers) are heavily calcified parts in callianasids and, in consequence, are the ones most often found as fossils (Hyžný & Klompmaker, 2015) (Fig. 6S–U).

Finally, a discinid brachiopod (N=1, *Discinisca porvenir*, CNP-PIIc 594; Fig. 3A, B) preserves its original organophosphatic shell material with minimal damage (see Pérez et al., 2023 for further details).

DISCUSSION

Previous knowledge of fossil invertebrate assemblages at Bryn Gwyn

Based on our findings, the Bryn Gwyn invertebrate assemblage is now composed of 27 genus or species-level taxa, and one family-level taxon (Crassatellidae), increasing nearly two times the known fossil fauna for the locality. Major groups previously recognized by non-precise determinations (bryozoans, gastropod molds, irregular echinoids) are now determined at the generic or specific level. Moreover, two non-previously reported major groups are added (Brachiopoda and Scaphopoda) (Tabs. 1, 2).

The studied assemblage is taxonomically dominated by gastropods (11 species), followed by bivalves (10 species), echinoderms (two species), and a single one of brachiopods, bryozoans, scaphopods, and arthropods.

Taphonomic observations

Notably, many of the previous mentions of taxa in Bryn Gwyn are based on molds (*e.g.*, Scasso & Bellosi, 2004; Cuitiño et al., 2019; del Río et al., 2021). This is probably one of the main reasons why, to this day, much of this fauna is referred to as large general groups (such as "bivalves", "gastropods", or "veneroids"). Because of this, we include preliminarly observations on taphonomy and preservation of the studied material.

The observed spectrum of preservation styles indicates that multiple physico-chemical and biological factors influenced the fossilization of the Bryn Gwyn invertebrates. The dominance of molds and recrystallized shells throughout the stratigraphic succession suggests chemical alterations during the early diagenesis. In particular, recrystallized shells, together with evidence of encrustation and bioerosion on specimens preserved within Level 6, indicate post-mortem infestation prior to chemical alteration during relatively long exposure times at the water-sediment interface. In addition, this level hosts the highest diversity and abundance of taxa within the succession, displaying contrasting preservational styles that reflect intrinsic paleobiological features and ecological controls (*e.g.*, infaunal vs. epifaunal life habits) that may have conditioned fossilization. For example, the presence of internal septa in echinoid tests confers greater structural strength against fragmentation, a reminder that fragmentation itself—like disarticulation—can be a problematic variable due to both paleobiological traits and collecting/processing biases (Best & Kidwell, 2000). Likewise, brachiopods with delicate organophosphatic shells, in contrast to those invertebrates with carbonate shells, follow clearly different taphonomic pathways. In other words, distinct groups with contrasting

TABLE 1. Previous lists of the invertebrate fossils in the Bryn Gwyn area.

Ihering 1904, 1907	Frenguelli 1927, 1935	Simpson (1935)	Feruglio (1949)
Turritella ambulacrum pyramidesia *Ostrea patagonica* *Chione patagonica* *Martesia patagonica* *Monophora darwini*	*Polinices* sp. *Turritella ambulacrum* *Pectunculus cuevensis* *Ostrea hatcheri* *Ostrea patagonica* *Sanguinolaria perplana* *Chione argentina*	*Ostrea hatcheri* "mollusks/shells" crabs	"*Turritella*" *ambulacrum* *Ostrea hatcheri* Internal molds of gastropod and bivalves
Camacho and Fernandez (1956)	**Haller and Mendía (1980)**	**Scasso and Castro (1999)**	**Scasso and Bellosi (2004)**
Ostrea maxima *Venericardia* (*Venericor*) *austroplata*	Gastropod molds *Ostrea hatcheri* *Ostrea maxima* *Venericardia* Pelecypod molds *Balanus* sp. Echinoids Crab remains	*Turritella* *Ostrea*/Oysters Pectinids *Venericardia* Echinoids *Callianasa* sp.	*Turritella* Gastropods Oysters Bivalves
Cuitiño et al. (2019)	**del Río et al. (2021)**		
Corals Bryozoans *Turritella* sp. Gastropods Oysters Pectinids Veneroids Irregular echinoids Barnacles	Pectinid molds Venerid molds Pholadidean molds		

intrinsic properties are preserved within the same stratigraphically condensed level, but through different styles—some as molds, others recrystallized, and others retaining original shell material. In contrast, Levels 1 and 7 contain fewer taxa but exhibit exceptional preservation (*e.g.*, pristine *Discinisca*, articulated *Macoma*), suggesting a brief biostratinomic period, characterized by rapid burial and short residence times at the sediment–water interface.

These patterns underline the interplay of biological (*i.e.*, shell composition, ecological preferences) and physicochemical factors (*i.e.*, water energy, sedimentation rate, geochemical features) in controlling the quality of the Bryn Gwyn fossil invertebrates. These observations are very preliminary but emphasize the need for a more detailed taphonomic survey of fossil invertebrates, not only through systematic recording of each taphonomic attribute during *in situ* fieldwork, but also by comparing shell microstructure and composition in relation to palaeoenvironmental settings, assessing their resistance to mechanical destructive processes, as well as the geochemical conditions leading to dissolution or mineral replacement.

Comparisons with other marine Cenozoic invertebrate assemblages of Patagonia

Comparisons of the updated invertebrate faunal list of the Gaiman Formation at Bryn Gwyn with those from other Paleogene and Neogene marine units of Patagonia allow us to rank their similarities. The highest similarities are shared with the Lower Miocene Chenque and Monte León formations (55% of genera) (Fig. 7; Supplementary Information 1, Tab. S1) (see Cuitiño et al., 2015a, 2023; Parras et al., 2012; Parras & Cuitiño, 2021; Genge et al., 2022). Following the latter in order of similarity are the Lower Miocene El Chacay Formation (37% of genera) (Cuitiño et al., 2015b) and the late Oligocene San Julián Formation (37% of genera) (Parras et al., 2012). Other units generally considered coeval with the Gaiman Formation, such as the Gran Bajo del Gualicho, Vaca Mahuida, Estancia 25 de Mayo, and Carmen Silva formations (Parras & Cuitiño, 2021; Kronemberger et al., 2025) show a reduced number of shared taxa (between 26 and 4% of genera), probably because of the incomplete knowledge of the bearing invertebrate assemblages. The case of the Vaca Mahuida

TABLE 2. Previous list of the invertebrate fossils in the Bryn Gwyn area.

Until now	This paper
-	*Discinisca porvenir*
Bryozoans	*Discoporella* sp.
Polinices sp.	*Glossaulax*? cf. *G. secundum*
Gastropod molds	*Molvaldesia* cf. *M. astraensis*
	Buccinanops halleri sp. nov.
	Miomelon gracilior
	Pachycymbiola camachoi
	Perissodonta ameghinoi
	Zeacuminia santacruzensis
	Penion subrectus
	Aeneator annae
"*Turritella*" *ambulacrum*	"*Turritella*" *ambulacrum*
	"*Torcula*" cf. "*T.*" *hauthali*
Pectunculus cuevensis	*Glycymerita camaronesia*
Crassostrea? *hatcheri*	*Crassostrea*? *hatcheri*
-	*Plicatula* sp.
Venericardia (*Venericor*) *austroplata*	*Neovenericor camachoi*
-	*Patagonicardium philippi*?
Chione patagonica/ *Chione argentina*/	*Ameghinomya argentina*
Bivalve molds	*Austrocallista iheringi*
	Retrotapes ninfasiensis
Martesia patagonica (possibly)	*Cyrtopleura lanceolata*
-	*Fissidentalium*? sp.
Irregular echinoids/ *Monophora darwini*	*Amplaster alatus*
Echinoids	*Brisaster iheringi*
Callianasa sp.	*Callianasa* sp.

Formation is striking because, beyond the carditid genus *Neovenericor* (Pérez et al., 2025), no other fossil invertebrate is mentioned.

In levels of the Chenque Formation, del Río (2004) recognized a molluscan assemblage zone named NVG (*Nodipecten* sp.-*Venericor abasolensis*-*Glycymerita camaronesia*). This assemblage includes as key or abundant taxa *Glycymerita camaronesia*, "*Venericor*" (=*Neovenericor*), "*Valdesia*" *astraensis* (*Molvaldesia astraensis*), or *Ameghinomya argentina*, all of them present in the Bryn Gwyn association. In addition, the NVG assemblage includes species of the genera *Pachycymbiola* and *Retrotapes*, and the long-ranging taxa "*Polinices*" *secunda* (=*Glossaulax secundum*), "*Turritella*" *ambulacrum*, "*Torcula*" *hauthali*, *Struthiolarella ornata* (=*Perissodonta ameghinoi*), *Penion subrectus*, and *Austrocallista iheringi*; all these taxa are also present in the Bryn Gwyn locality. The shared invertebrate groups allow us to recognize the presence of the NVG assemblage zone (del Río, 2004) in the Bryn Gwyn studied

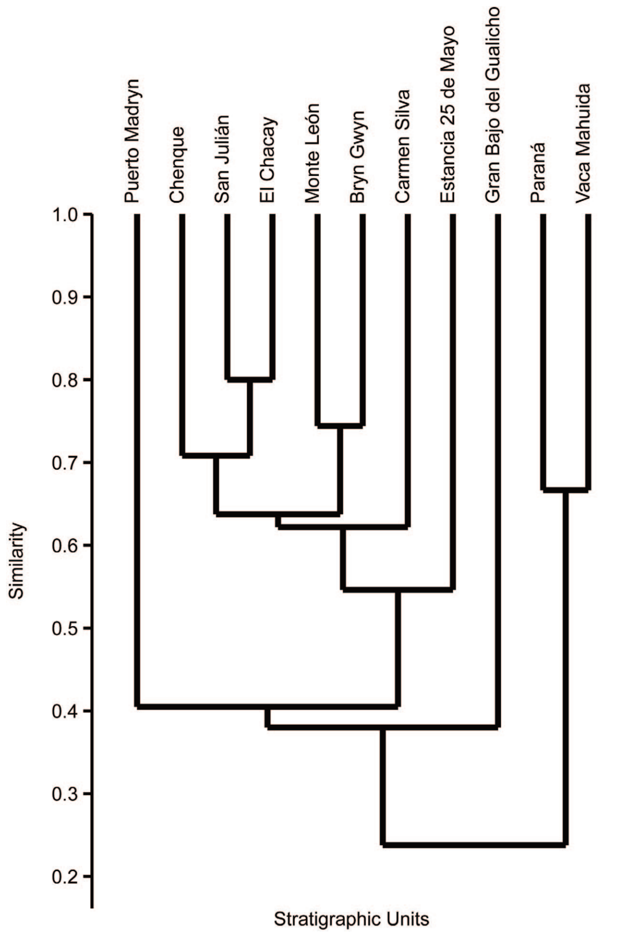

Figure 7. Cluster analysis showing similarity between the invertebrate faunal assemblage of Bryn Gwyn and different Cenozoic marine stratigraphic units.

levels. A latest Early Miocene to earliest middle Miocene age was attributed to this assemblage zone (del Río, 2004; del Río et al., 2022b). Considering that most of the taxa here reported come from the upper part of the studied section (Level 6) we can suggest matching our assemblage with the NVG zone.

CONCLUSIONS

The new fossil marine invertebrate sample here described for the Gaiman Formation at the Bryn Gwyn locality comprise 27 genera or species-level taxa, being the first record for the Gaiman Formation of the genera *Discoporella*, *Molvaldesia*, *Glossaulax*, *Buccinanops*, *Miomelon*, *Pachycymbiola*, *Perissodonta*, *Zeacuminia*, "*Torcula*", *Penion*, *Aeneator*, *Plicatula*, *Patagonicardium*, *Ameghinomya*, *Austrocallista*, *Retrotapes*, *Cyrtopleura*, *Fissidentalium*, *Amplaster*, and *Brisaster*. The new species *Buccinanops halleri* represents the oldest record for the genus. In addition, two major groups are recorded for the first time in the studied area: Brachiopoda and Scaphopoda.

In comparison to other Cenozoic marine invertebrate assemblages of Patagonia, the Bryn Gwyn fauna is more similar to that of the Chenque and Monte León formations. These units are also considered to have been deposited during the "Patagonian Transgression" and present coeval ages.

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REFERENCES

Agnolín, F., Bogan, S., Lucero, S., Chimento, N. R., Santelli, M. B., Alvarez, M. J., Pérez, D., & Gambetta, D. H. (2024). Vertebrados e invertebrados fósiles en la Costa Atlántica de la provincia de Buenos Aires, Argentina: Edad y paleoambientes. *Acta Geológica Lilloana*, *35*(1), 37–99.

Aguirre, M. L., & Farinati, E. A. (2000). Moluscos marinos del Cuaternario de Argentina. *Boletín de la Academia Nacional de Ciencias*, *64*, 236–333.

Aguirre, M. L., Richiano, S., & Sirch, Y. N. (2006). Palaeoenvironments and palaeoclimates of the Quaternary molluscan faunas from the coastal area of Bahía Vera–Camarones (Chubut, Patagonia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *229*(4), 251–286.

Aguirre-Urreta, M. B. (1990). Nuevos crustáceos decápodos (Brachyura y Anomura) en el Terciario de Patagonia, Argentina. *Serie Correlación Geológica*, *7*, *Actas del 5° Congreso Argentino de Paleontología y Bioestratigrafía* (pp. 149–154). Tucumán.

Allende Mosquera, A., Cuitiño, J. I., & Espinosa, M. A. (2023). Fossil diatom study reveals significant freshwater input in Miocene coastal marine environments of the southwestern Atlantic (Patagonia, Argentina). *Ameghiniana*, *60*(4), 342–357.

Allmon, W. D., & Knight, J. L. (1993). Paleoecological significance of a turritelline gastropod-dominated assemblage in the Cretaceous of South Carolina. *Journal of Paleontology*, *67*(3), 355–360.

Alvarez, M. J. (2019). Phylogenetic analysis of the genus *Retrotapes* del Río, 1997 (Bivalvia: Veneridae) and systematic analysis of its taxa from Chile. *Journal of Paleontology*, *93*(4), 685–701.

Alvarez, M. J., del Río, C. J., & Martínez, S. (2020). Revision of the subfamily Pitarinae Stewart, 1930 (*Eucallista* Dall, 1902; *Austrocallista* Erdmann & Morra, 1985; *Proteopitar* gen. nov.) from Cenozoic southern South America: Systematic and phylogenetic analyses. *Journal of Systematic Palaeontology*, *18*(5), 433–460.

Ameghino, F. (1901). L'age des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina*, *52*, 189–197.

Bałuk, W., & Radwański, A. (1982). Middle Miocene (Badenian) free-living bryozoans from the Vienna Basin. *Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie*, *86*, 13–40.

Bellosi, E., & Barreda, V. D. (1993). Secuencias y palinología del Terciario medio en la Cuenca San Jorge: Registro de oscilaciones eustáticas en Patagonia. *Actas del 12° Congreso Geológico Argentino y 2° Congreso de Exploraciones de Hidrocarburos*, (Vol. 1, pp. 78–86). Mendoza.

Bengtson, P. (1988). Open nomenclature. *Palaeontology*, *31*(1), 223–227.

Best, M. M., & Kidwell, S. M. (2000). Bivalve taphonomy in tropical mixed siliciclastic–carbonate settings. I. Environmental variation in shell condition. *Paleobiology*, *26*(1), 80–102.

Beu, A. G., Griffin, M., & Maxwell, P. A. (1997). Opening of Drake Passage gateway and Late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: Evidence from New Zealand and Argentina. *Tectonophysics*, *281*, 83–97.

Blainville, H. M. D. de. (1814). Sur la classification méthodique des animaux mollusques, et établissement d'une nouvelle considération pour y parvenir. *Bulletin des Sciences, par la Société Philomatique de Paris*, 175–180.

Bostelmann, E., Ugalde, R., Oyarzún, J., & Griffin, M. (2015). The Patagonian transgression, early Miocene (Burdigalian age), in Aysén and Magallanes. *Actas del XIV Congreso Geológico Chileno*, Vol. 1, (pp. 825–828). La Serena.

Brito, C. (2009). *Evolución de las comunidades de organismos incrustantes y perforantes asociadas a arrecifes de ostras gigantes del Paleógeno y Neógeno de Patagonia, Argentina* [Bachelor's Degree Thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa]. https://repo.unlpam.edu.ar/handle/unlpam/2183

Broderip, W. J. (1833). Descriptions of some new species of Cuvier's family of Brachiopoda. *Proceedings of the Zoological Society of London*, *1*, 124–125.

Bronn, H. G. (1862). *Die Klassen und Ordnungen der Weichthiere (Malacozoa), wissenschaftlich dargestellt in Wort und Bild. Dritten Bandes erste Abtheilung. Kopflose Weichthiere (Malacozoa Acephala).* C. F. Winter.

Brunet, R. F. (1995). New species of Mollusca from the Entrerriense Formation (Upper Miocene) of Chubut Province, Argentina, and species not previously reported from the formation. Part I – Gastropoda and Scaphopoda. *Tulane Studies in Geology and Paleontology*, *28*(1–2), 1–56.

Buono, M. R., Fernández, M. S., Cozzuol, M. A., Cuitiño, J. I., & Fitzgerald, E. M. G. (2017). The early Miocene balaenid *Morenocetus parvus* from Patagonia (Argentina) and the evolution of right whales. *PeerJ*, *5*, e4148.

Busk, G. (1852). An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago. In J. MacGillivray (Ed.), *Narrative of the voyage of H.M.S. Rattlesnake* (Vol. 1, pp. 343–402). T. & W. Boone.

Cabrera, A. (1928). Notas sinonímicas sobre algunas ostras fósiles sudamericanas. *Revista Chilena de Historia Natural*, *32*, 13–21.

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

Camacho, H. H. (1981). *Neovenericor*, un sinónimo de *Venericardia* (*Venericor*) (Mollusca, Bivalvia). *Revista de la Asociación Geológica Argentina*, *36*(3), 312–318.

Camacho, H. H., & Fernandez, J. A. (1956). La transgresión patagoniense en la costa atlántica entre Comodoro Rivadavia y el curso inferior del río Chubut. *Revista de la Asociación Geológica Argentina*, *11*(1), 23–45.

Camacho, H. H., & Zinsmeister, W. (1989). La Familia Struthiolariidae Fischer, 1884 (Mollusca: Gastropoda) y sus representantes del Terciario Patagónico. *Actas del 48° Congreso Argentino de Paleontología y Bioestratigrafía* (pp. 99–110). Mendoza.

Canu, F. (1904). Les bryozoaires du Patagonien. Échelle des bryozoaires pour les terrains tertiaires. *Mémoires de la Société Géologique de France: Paléontologie*, *12*, 1–30.

Carmona, N. B., Mángano, M. G., Buatois, L. A., & Ponce, J. J. (2007). Bivalve trace fossils in an early Miocene discontinuity surface in Patagonia, Argentina: Burrowing behavior and implications for ichnotaxonomy at the firmground-hardground divide. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *255*(3–4), 329–341.

Casadío, S., & Griffin, M. (2009). Sedimentology and paleontology of a Miocene marine succession first noticed by Darwin at Puerto Deseado (Port Desire). *Revista de la Asociación Geológica Argentina*, *64*(1), 83–89.

Casadío, S., Håkansson, E., Parras, A., & Griffin, M. (2005). Free-living bryozoans in the late Miocene Puerto Madryn Formation, Península Valdés: Paleoenvironmental and paleobiogeographical implications. *Ameghiniana*, *42*(4 Suppl.), 20R.

Children, J. G. (1834). [Mollusca]. In British Museum (Ed.), *Synopsis of the contents of the British Museum* (ed. 28, pp. 88–118). British Museum

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 conexos. *Ameghiniana*, *15*, 183–208.

Cione, A. L., & Azpelicueta, M. (2003). An Oplegnathid beak (Osteichthyes: Perciformes) from the Early Miocene of Patagonia. Extirpation of several vertebrates from southern Atlantic Ocean. *Geobios*, *36*(5), 625.

Cione, A. L., Cozzuol, M. A., Dozo, M. T., & Acosta Hospitaleche, C. (2011). Marine vertebrate assemblages in the southwest Atlantic during the Miocene. *Biological Journal of the Linnean Society*, *103*(2), 423–440.

Clench, W. J., & Turner, R. D. (1964). The subfamilies Volutinae, Zidoninae, Odontocymbiolinae and Callioctectinae in the western Atlantic. *Johnsonia*, *4*(43), 129–179.

Closs, D., & Madeira, M. (1968). Cenozoic Foraminifera from the Chuy drill hole, northern Uruguay. *Ameghiniana*, *5*, 229–246.

Conrad, T. A. (1841). Appendix to Mr. Hodge's paper, describing the new shells. *American Journal of Science*, *41*(2), 344–348.

Cook, P., & Chimonides, P. (1994). Notes on the family Cupuladriidae (Bryozoa), and on *Cupuladria remota* sp. n. from the Marquesas Islands. *Zoologica Scripta*, *23*(3), 251–268.

Cossmann, M. (1898). Mollusques éocéniques de la Loire-inférieure. Appendice au second fascicule. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, *8*, 1–55.

Cossmann, M. (1901). *Essais de Paléoconchologie Comparée* (Vol. 4). N.p.

Cotton, B. C., & Godfrey, F. K. (1938). *A systematic list of the gastropoda the marine, freshwater and land univalve mollusca of south and central Australia*. Malacological Society of South Australia.

Cox, L. R. (1960). Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London*, *33*(6), 239–261.

Cuitiño, J. I., Scasso, R. A., Ventura Santos, R., & Mancini, L. (2015a). Sr ages for the Chenque Formation in the Comodoro Rivadavia region (Golfo San Jorge Basin, Argentina): Stratigraphic implications. *Latin American Journal of Sedimentology and Basin Analysis*, *22*, 3–12.

Cuitiño, J. I., Ventura Santos, R., Alonso Muruaga, P. J., & Scasso, R. A. (2015b). Sr-stratigraphy and sedimentary evolution of early Miocene marine foreland deposits in the northern Austral (Magallanes) Basin, Argentina. *Andean Geology*, *42*(3), 364–385.

Cuitiño, J. I., Buono, M. R., Viglino, M., Farroni, N., & Bessone, S. (2019). Factors affecting the preservation and distribution of cetaceans in the lower Miocene Gaiman Formation of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *526*, 110–125.

Cuitiño, J. I., Bilmes, A., Buono, M. R., Bordese, S., Herazo, L., & Scasso, R. A. (2023). Stratigraphy, provenance, and timing of Neogene sedimentation in the western Valdés Basin, Patagonia. Accurate paleogeographic reconstructions as a key piece for andean-passive margin integration. *Journal of South American Earth Sciences*, *124*, 104278.

Cuitiño, J. I., Pérez, D. E., Farroni, N. D., Allende Mosquera, A., Viglino, M., Buono, M. R., & Scasso, R. A. (In press). Depositional environments, fossil content and stratigraphy of the Miocene marine succession at Bryn Gwyn and nearby localities, northeast Chubut, Patagonia, In M. R. Buono & M. E. Pérez (Eds.), *The Vertebrate Paleontology from the Cenozoic of Bryn Gwyn, Gaiman (Patagonia, Argentina)*. Springer Earth Systems Series.

Cuvier, G. (1795). Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique. Journal des Sciences, des Lettres et des Arts*, *2*, 433–449.

d'Orbigny, A. D. (1834–1847). *Voyage dans l'Amérique méridionale (le Brésil, la république orientale de l'Uruguay, la République Argentine, la Patagonie, la république du Chili, la république de Bolivia, la république du Pérou), exécuté pendant les années 1826–1833. Tome 5(3), Mollusques*. Pitois-Levrault, V. Levrault.

d'Orbigny, A. D. (1851). *Paléontologie française. Terrains Crétacés. Tome V, Bryozoaires*. Victor Masson.

d'Orbigny, A. D. (1852). *Paléontologie française. Terrains Jurassiques. Tome II, Gasterópodes*. Victor Masson.

Dall, W. H. (1871). Report on the Brachiopoda of the Straits of Florida, in Charge of L. F. de Pourtales, with a Revision of the Craniidae and Discinidae Obtained by the U. S. Coast Survey Expedition. *Bulletin of the Museum of Comparative Zoology at Harvard University*, *3*, 1–45.

Dall, W. H. (1907). A review of the American Volutidae. *Smithsonian Miscellaneous Collections*, *48*, 341–373.

Dall, W. H. (1908). Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. XXXVII. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross", from October, 1904 to March, 1905, Lieut.-Commander L.M. Garrett, U.S.N., commanding. XIV. The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology*, *43*(6), 205–487.

Dall, W. H. (1925). Note on the Atlantic Coast species of *Plicatula*. *Proceedings of the Biological Society of Washington*, *38*, 90.

Dana, J. D. (1852). Conspectus crustaceorum, &c. Conspectus of the Crustacea of the exploring expedition under Capt. C. Wilkes, U.S.N. Macroura. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *6*, 10–28.

Defrance, J. L. M. (1823). Polypiers. In F. Cuvier (Ed.), *Dictionnaire des Sciences Naturelles* (pp. 265–271). F. G. Levrault.

de Loriol, P. (1902). *Notes pour servir a l' étude des échinodermes* (2) 1. Bale et Geneve (Librairie Georg et cie.).

de Mata, O. (1947). *La formación holocena en el Departamento de Montevideo (República Oriental del Uruguay)*. Imprenta Nacional.

del Río, C. J. (1985). Primera mención de la subfamilia Architectonicinae (Mollusca: Gastropoda) en el Terciario de la Patagonia (República Argentina). *Ameghiniana*, *22*(3–4), 263–268.

del Río, C. J. (1992). Middle Miocene Bivalves of the Puerto Madryn Formation, Valdés Peninsule, Chubut Province, Argentina (Nuculidae-Pectinidae), Part I. *Palaeontographica Abteilung A*, *225*, 1–57.

del Río, C. J. (1997). Cenozoic biogeographic history of the eurothermal genus *Retrotapes* n. gen. (Subfamily Tapetinae) from Southern South America and Antarctica. *The Nautilus*, *110*(3), 77–93.

del Río, C. J. (2004). Tertiary Marine molluscan assemblages of eastern Patagonia (Argentina): A biostratigraphic analysis. *Journal of Paleontology*, *78*(6), 1097–1122.

del Río, C. J. (2021). Paleoclimate and changing composition of the Paleogene-Neogene shallow Molluscan Assemblages of Patagonia. *Journal of South American Earth Sciences*, *108*, 103209.

del Río, C. J., & Camacho, H. H. (1998). Tertiary nuculoids and arcoids of Eastern Patagonia (Argentina). *Palaeontographica, Abteilung A*, *250*, 47–88.

del Río, C. J., & Martínez, S. (1998). Clase Bivalvia. In C. J. del Río (Ed.), *Moluscos Marinos Miocenos de la Argentina y Uruguay* (Vol. 15, pp. 48–83). Academia Nacional de Ciencias Exactas, Físicas y Naturales.

del Río, C. J., & Martínez, S. (2006). The family Volutidae (Mollusca-Gastropoda) in the Tertiary of Patagonia (Argentina). *Journal of Paleontology*, *80*, 919–945.

del Río, C. J., Concheyro, A., & Martínez, S. (2011). The Maastrichtian–Danian at General Roca: A reappraisal of the chronostratigraphy and biostratigraphy of a type locality (Patagonia, Argentina). *Neues Jahrbuch für Geologie und Paläontologie*, *259*, 129–156.

del Río, C. J., Martínez, S., & Scasso, R. A. (2001). Nature and origin of spectacular marine Miocene shell beds of northeastern Patagonia (Argentina): Paleoecological and bathymetric significance. *Palaios*, *16*, 3–25.

del Río, C. J., Martínez, S., McArthur, J., Thirlwall, M., & Pérez, L. M. (2018). Dating late Miocene marine incursions across Argentina and Uruguay with Sr-isotope stratigraphy. *Journal of South American Earth Sciences*, *85*, 312–324.

del Río, C. J., Martínez, S., Griffin, M., & De Francesco, C. G. (2022a). Moluscos y Equinodermos del Paleógeno-Neógeno. In R. Giacosa (Ed.), *Relatorio del XXI Congreso Geológico Argentino, geología y Recursos Naturales de la Provincia del Chubut* (pp. 1005–1028). Asociación Geológica Argentina.

del Río, C. J., Bellosi, E., McArthur, J., & Thirlwall, M. (2022b). Early Miocene Sr-geochronology of Patagoniense marine units from southern Argentina: Implications for molluscan assemblages and interbasinal correlation. *Journal of South American Earth Sciences*, *120*, 104097.

Deshayes, G. P. (1839). Nouvelles espèces de mollusques, provenant des côtes de la Californie, du Mexique, du Kamtschatka et de la Nouvelle-Zélande. *Revue Zoologique par la Société Cuvierienne*, *2*(12), 356–361.

Desor, E. (1847). Sur quelques oursins fossiles de la Patagonie. *Bulletin de la Société Géologique de France, Series 2*, *4*, 287–288.

DeVries, T. (2007). Cenozoic Turritellidae (Gastropoda) from Southern Peru. *Journal of Paleontology*, *81*(2), 331–351.

Dillwyn, L. W. (1817). *A descriptive catalogue of Recent shells, arranged according to the Linnean method; with particular attention to the synonymy* (Vols. 1–2, pp. 1–1092 + index 29 pp.). John and Arthur Arch.

Düben, M. W. von, & Koren, J. (1846). Öfversigt af Skandinaviens Echinodermer [Overview of Scandinavian Echinodermata]. *Kungl. Svenska Vetenskapsakademiens Handlingar*, *1844*, 229–328. [In Swedish].

Duméril, A. M. C. (1805). *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Allais.

Erdmann, S., & Morra, G. A. (1985). Nuevos moluscos de la Formación San Julián, provincia de Santa Cruz. *Ameghiniana*, *22*(3–4), 289–295.

Farroni, N. D., Cuitiño, J. I., Pérez, D. E., & Buono, M. R. (2023). Sedimentological and stratigraphically controlled preservation styles and distribution of fossil cetaceans from a new Early Miocene fossiliferous locality, Patagonia, Argentina. *Historical Biology*, *36*(7), 1328–1342.

Feruglio, E. (1949). *Descripción Geológica de la Patagonia* (Vols. 1–2). Ministerio de Industria y Comercio de La Nación, Dirección General de Yacimientos Petrolíferos Fiscales.

Férussac, A. (1822). *Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; survis d'un prodrome général por tous les mollusques terrestres ou fluviétiles, vivants ou fossiles*. Chez Arthus Bertrand.

Figueiras, A. (1980). Los braquiópodos fósiles del Uruguay. Comunicación preliminar sobre los braquiópodos del Terciario. *Resúmenes de las 1ras Jornadas de Ciencias Naturales* (pp. 89–90). Montevideo.

Finlay, H. (1926). A further commentary on New Zealand molluscan systematics. *Transactions of the New Zealand Institute*, *57*, 320–485.

Finlay, H. (1930). Invalid molluscan names. No. 1. *Transactions of the New Zealand Institute*, *61*, 37–48.

Finlay, H., & Marwick, J. (1937). The Wangaloan and associated molluscan faunas of Kaitangata-Green Island subdivision. *New Zealand Department of Scientific and Industrial Research, Geological Survey Branch, Palaeontological Bulletin*, *15*, 1–140.

Fischer, P. (1880–1887). *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossiles suivi d'un Appendice sur les Brachiopodes par D. P. Oehlert. Avec 23 planches contenant 600 figures dessinées par S. P. Woodward.* F. Savy.

Frassinetti, D. (2001). Moluscos bivalvos y gastropodos del Mioceno marino de Isla Stokes, Sur de Chile. *Boletín del Museo Nacional de Historia Natural de Chile*, *50*, 73–90.

Frassinetti, D. (2006). Moluscos fósiles del Mioceno marino de Islas Crosslet y Hereford (Golfo Tres Montes, Aisén, Chile). *Boletín del Museo Nacional de Historia Natural de Chile*, *55*, 61–74.

Frassinetti, D., & Covacevich, V. (1999). Invertebrados fósiles marinos de la Formación Guadal (Oligoceno Superior–Mioceno Inferior) en Pampa Castillo, Región de Aisén, Chile. *Servicio Nacional de Geología y Minería, Boletín*, *51*, 1–96.

Frenguelli, J. (1927). El Entrerriense de Golfo Nuevo en el Chubut. *Boletín de la Academia Nacional de Ciencias*, *29*, 191–270.

Frenguelli, J. (1935). El perfil de Gaiman, Chubut. *Notas del Museo de La Plata. Geología*, *1*, 177–192.

Friend, D., Anderson, B., Altier, E., Sang, S., Petsios, E., Portell, R., & Allmon, W. (2023). Systematics and phylogeny of Plio-Pleistocene species of Turritellidae (Gastropoda) from Florida and the Atlantic Coastal Plain. *Bulletins of American Paleontology*, *402*, 1–74.

Galindo, L. A., Puillandre, N., Utge, J., Lozouet, P., & Bouchet, P. (2016). The phylogeny and systematics of the Nassariidae revisited (Gastropoda, Buccinoidea). *Molecular Phylogenetics and Evolution*, *99*, 337–353.

Gardner, J., & Bowles, E. (1939). The *Venericardia planicosta* group in the Gulf Province. *United States Geological Survey, Professional Paper*, 189-F, 141–215.

Garvie, C. L. (1996). The molluscan macrofauna of the Reklaw Formation, Marquez Member (Eocene: Lower Claibornian), in Texas. *Bulletins of American Paleontology, 111*(352), 1–177.

Genge, M. C., Zattin, M., Witt, C., Derycke, A., Gautheron, C., Mazzoli, S., Petrelli, M., Cogné, N., Bosch, D., Bruguier, O., & Marquez, M. (2022). Denudation of the Cordillera and intraplate belt in Central Patagonia inferred by detrital multi-dating of foreland basin deposits. *Sedimentary Geology*, *440*, 106237.

Genta Iturrería, S., & Griffin, M. (2018). A review of the South American members of the family Struthiolariidae Fischer. *Publicación Electrónica de la Asociación Paleontológica Argentina*, *19*(1), R52.

Gmelin, J. F. (1791). Vermes. In J. F. Gmelin (Ed.), *Caroli a Linnaei Systema Naturae per Regna Tria Naturae* (13th ed., Vol. 1(6), pp. 3021–3910). G. E. Beer.

Gravenhorst, J. L. C. (1843). *Vergleichende Zoologie*. Graß, Barth & Comp.

Gray, J. E. (1840). Shells of molluscous animals. *Synopsis of the contents of the British* Museum, *42*, 106–156.

Gray, J. E. (1850). *Figures of molluscous animals, selected from various authors* (Vol. 4). Longman, Brown, Green and Longmans.

Gray, J. E. (1854). Additions and corrections to the arrangement of the families of bivalve shells. *The Annals and Magazine of Natural History, Series 2*, *14*(79), 21–28.

Gray, J. E. (1855). *Catalogue of the Recent Echinida, or Sea Eggs, in the Collection of the British Museum. Part I.-Echinida Irregularia*. Woodfall & Kinder.

Griffin, M., & Nielsen, S. (2008). A revision of the type specimens of Tertiary molluscs from Chile and Argentina described by d'Orbigny (1842), Sowerby (1846) and Hupé (1854). *Journal of Systematic Palaeontology*, *6*(3), 251–316.

Griffin, M., & Pastorino, G. (2013). Cenozoic Ampullinidae and Naticidae (Mollusca, Gastropoda) from Patagonia, Argentina. *Journal of Paleontology*, *87*, 502–525.

Guilding, L. (1834). Observations on *Naticina* and *Dentalium*, two genera of molluscous animals. *Transactions of the Linnean Society of London*, *17*(1), 29–35.

Haller, M. J., & Mendía, J. E. (1980). Las sedimentitas del ciclo Patagoniano en el litoral atlántico norpatagónico. *Actas del 8° Congreso Geológico Argentino* (Vol. 3, pp. 593–606). San Luis.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologica Electronica*, *4*(1), 1–9.

Hupé, L. H. (1854). Fauna Chilena. In C. Gay (Ed.), *Historia Física y Política de Chile. Zoología* (Vol. 8, pp. 1–407). Maulde & Renou.

Hyžný, M., & Klompmaker, A. (2015). Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Systematics & Phylogeny*, *73*(3), 401–437.

Ihering, H. von (1896). Zur Kenntnis der südamerikanischen Voluta und ihrer Geschichte. *Nachrichtsblätter Deutsche Malakozoologische Gesellschaft*, *7*, 93–99.

Ihering, H. von (1897). Os molluscos dos terrenos terciarios da Patagonia. *Revista do Museo Paulista*, *2*, 217–382.

Ihering, H. von (1899). Die Conchylien der patagonischen Formation. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie*, *2*, 1–41.

Ihering, H. von (1903). Les brachiopodes tertiaires de Patagonie. *Anales del Museo Nacional de Buenos Aires (Serie 3°, II)*, *9*, 321–349.

Ihering, H. von (1904). Nuevas observaciones sobre moluscos cretáceos y terciarios de Patagonia. *Revista del Museo de La Plata*, *11*, 229–243.

Ihering, H. von (1907). Les Mollusques fossiles du Tertiaire et du Cretace Superieur de l'Argentine. *Anales del Museo Nacional de Buenos Aires (Serie 3)*, *14*(7), 1–611.

Jeffreys, J. G. (1877). New and peculiar Mollusca of the order Solenoconchia procured during the Valorous expedition. *Annals and Magazine of Natural History*, *(4)*19, 154–158.

Kay, R. F., Fleagle, J. G., Mitchell, T. R. T., Colbert, M., Bown, T., & Powers, D. W. (2008). The anatomy of *Dolichocebus gaimanensis,* a stem platyrrhine monkey from Argentina. *Journal of Human Evolution*, *54*, 323–382.

Kiener, L. C. (1834–1841). *Spécies général et iconographie des coquilles vivantes*. *Famille des Purpurifères* (Deuxième partie). J. B. Baillière.

King, P. P. (1832). Description of the Cirrhipeda, Conchifera and Mollusca, in a collection formed by the officers of H.M.S. Adventure and Beagle employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens and the coast of Tierra del Fuego. *Zoological Journal*, *5*(125), 332–349.

Klein, J. T. (1778). *Naturalis Dispositio Echinodermatum. Accessit Lucubratiuncula de Aculeis Echinorum Marinorum et Specilegium de Belemnitis*. Officina Gleditschiana.

Kronemberger, J. T., & Parras, A. (2024). Turritelline-dominated assemblages from the Monte León formation (Lower Miocene), Patagonia, Argentina: Paleoecological and paleoenvironmental implications. *Ameghiniana*, *61*(2), 118–137.

Kronemberger, J. T., Cuitiño, J. I., & Parras, A. M. (2025). Neogene Litho and Chronostratigraphy in the Southwestern Margin of the Colorado Basin (Río Negro, Argentina): The Gran Bajo Del Gualicho Formation. *Journal of South American Earth Sciences*, *153*, 105369.

Lagaaij, R. (1952). The Pliocene Bryozoa of the Low Countries and their bearing on the marine stratigraphy of the North Sea region. *Mededelingen van de Geologische Stichting*, *5*, 6–233.

Lahille, F. (1896). Variabilité et affinités du *Monophora darwini*. *Revista del Museo de La Plata*, *7*, 411–444.

Lamarck, J. -B. (M. de). (1801). *Systéme des animaux sans vertébres ou tableau général des classes, des orders et des genres de ces animaux*. Published by the Author and Deterville.

Lamarck, J. -B. (M. de). (1809). *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux* (Tome premier, I–XXV, 1–428; Tome second, 1–475). Dentu & the author.

Lamarck, J. -B. (M. de). (1811). Suite de la détermination des espèces de Mollusques testacés. Volute (*Voluta*). *Annales du Muséum d'Histoire Naturelle*, *17*, 54–80.

Lambert, J. (1905). Notes sur quelques Échinides éocéniques de l'Aude et de l'Hérault. In L. Doncieux (Ed.), *Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault. Première Partie. Montagne Noire et Minervois* (pp. 129–164). Annales de l'Université de Lyon, Nouvelle Série, I. Sciences, Médecine.

Latreille, P. A. (1802–1805). *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes. Familles naturelles des genre.* de L'imprimerie de F. Dufart.

Leach, W. E. (1813–1815). Crustaceology. In D. Brewster (Ed.), *The Edinburgh Encyclopaedia* (Vol. 7(1): 383–384 [1813]; 7(2): 385–437, 765–766 [1814]; 9(1): pl. CCXXI [1815]). Balfour.

Leach, W. E. (1819). A list of invertebrate animals discovered by H. M. S. Isabella, in a voyage to the Arctic regions: corrected by W. E. Leach. Appendix II. In J. Ross (Ed.), *A voyage of discovery in His Majesty's ships Isabella and Alexander (1818) for the purpose of exploring Baffin's Bay and enquiring into the possibility of a northwest passage* (pp. 61–64). John Murray.

Lech, R., Aceñolaza, F. G., & Grizinik, M. (2000). Icnofacies Skolithos-Ophiomorpha en el Neogeno del valle inferior del río Chubut, provincia del Chubut, Argentina. In F. G. Aceñolaza, & R. Herbst (Eds.), *El Neógeno de Argentina* (pp. 147–161). Instituto Superior De Correlación Geológica (INSUGEO).

Levy, R. (1961). Sobre algunos Terebratellidae de Patagonia (Argentina). *Ameghiniana*, *2*(5), 79–88.

Linnaeus, C. (1758). *Systema naturae per regna tria naturae* (Editio decima, reformata). Laurentii Salvii.

Linnaeus, C. (1764). *Museum s:æ r:æ m:tis Ludovicæ Ulricæ reginæ svecorum, gothorum, vandalorumque &c. &c. &c.* Published by the author.

Lopes, R. P., Simone, L. R., Dillenburg, S. R., Schultz, C. L., & Pereira, J. C. (2013). A middle Pleistocene marine molluscan assemblage from the Southern coastal plain of Rio Grande do Sul State, Brazil. *Revista Brasileira de Paleontologia*, *16*(3), 343–360.

López Cabrera, M. I., & Olivero, E. (2021). Intraspecific variability in the Early Miocene struthiolariid gastropod *Perissodonta ameghinoi* (Ihering, 1897) from Tierra del Fuego, Argentina. *Publicación Electrónica de la Asociación Paleontológica Argentina*, *21*(2), 34–52.

López-Gappa, J., Pérez, L. M., & Griffin, M. (2017). First record of a fossil selenariid bryozoan in South America. *Alcheringa*, *41*(3), 365–368.

Lóven, H. (1847). Malacozoologi. *Öfversigt af Kongliga Vetenskaps Akademiens Förhandlingar*, *4*, 175–199.

Marshall, P. (1917). The Wangaloa beds. *Transactions and Proceedings of the New Zealand Institute*, *49*, 450–460.

Martens, E. von. (1878). Ueber einige Conchylien aus den kälteren Meeresgegenden der südlichen Erdhälfte. *Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin*, 20–26.

Martínez, S. (1984). *Amplaster coloniensis n. g. sp. nov. (Echinoidea: Monophorasteridae) del Mioceno de Uruguay*. In P. M. del Carmen (Ed.), *Memoria III Congreso Latinoamericano de Paleontología* (pp. 505–508). Mexico.

Martínez, S., del Río, C. J., & Rojas, A. (2016). A Pleistocene (MIS 5e) mollusk assemblage from Ezeiza (Buenos Aires Province, Argentina). *Journal of South American Earth Sciences*, *70*, 174–187.

Martínez, S., & del Río, C. J. (2017). A supplementary description of *Brisaster iheringi* (Spatangoida: Schizasteridae) from the Miocene of Patagonia, Argentina. *Revista de Biología Tropical*, *65* (Suppl. 1), S137–S146.

Martínez, S., Manceñido, M. O., Pérez, L. M., & del Río, C. J. (2025). First occurrence of Lingulidae (?*Glottidia* Dall, 1870: Brachiopoda) in the Paraná Formation (Late Miocene, Argentina) and its implications. *Revista Brasileira de Paleontología*, *28*(2), e20250531.

Marwick, J. (1924). Palaeontological notes on some Pliocene Mollusca from Hawke's Bay. *Transactions and Proceedings of the New Zealand Institute*, *55*, 191–202.

MolluscaBase. (2025). *MolluscaBase*. Accessed at https://www.molluscabase.org on 2025-05-06.

Montagu, G. (1808). Description of several marine animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London*, *9*, 81–114.

Mörch, O. A. L. (1852). *Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra & Gadea Comes de Yoldi, Regis Daniae Cubiculariorum Princeps, Ordinis Dannebrogici in Prima Classe & Ordinis Caroli Tertii Eques. Fasc. 1, Cephalophora*. L. Klein.

Morra, G. A., & del Río, C. J. (1987). La Subfamili Architectonicinae (Mollusca: Gastropoda) en el Patagoniano. *Revista de la Asociación Geológica Argentina*, *42*, 82–91.

Murdoch, R. (1924). Some Tertiary Mollusca, with descriptions of new species. *Transactions of the New Zealand Institute*, *55*, 157–160.

Nielsen, S. (2003). *Die marinen Gastropoden (exclusive Heterostropha) aus dem Miozän von Zentralchile* [PhD Thesis, Universität Hamburg]. Retrieved from https://ediss.sub.uni-hamburg.de/bitstream/ediss/299/1/dissertation.pdf

Nielsen, S. (2005). Cenozoic Strombidae, Aporrhaidae, and Struthiolariidae (Gastropoda: Stromboidea) from Chile: their significance to the interpretation of southeast Pacific biogeography and climate. *Journal of Paleontology*, *79*(6), 1120–1130.

Nielsen, S., & Frassinetti, D. (2007). The Neogene Volutidae (Gastropoda: Neogastropoda) from the Pacific Coast of Chile. *Journal of Paleontology*, *81*(1), 82–102.

Nielsen, S., & del Río, C. J. (2022). A new name for *Valdesia* del Río 1985 (Cenozoic fossil Mollusca), junior homonym of *Valdesia* Maury, 1981 (extant Arachnida). *The Nautilus*, *136*(3–4), 70.

Ortmann, A. E. (1897). On some of the larger oysters of Patagonia. *The American Journal of Science*, *4*, 355–356.

Ortmann, A. E. (1900). Synopsis of the collections of Invertebrate fossils made by the Princeton Expedition to southern Patagonia. *The American Journal of Science*, *10*, 368–381.

Ortmann, A. E. (1902). Tertiary Invertebrates. In W. B. Scott (Ed.), *Reports of the Princeton University Expedition to Patagonia 1896–1899* (Vol. 4, Paleontology I, Part 2, pp. 32–45). J. Pierpoint Morgan Publishing Foundation.

Palazzesi, L., Vizcaíno, S., Barreda, V., Cuitiño, J., del Río, C., Goin, F., González Estebenet, M. S., Guler, M. V., Gandolfo, M. A., Kay, R., Parras, A., Reguero, M., & Zamaloa, M. (2021). Reconstructing Cenozoic Patagonian biotas using multi-proxy fossil records. *Journal of South American Earth Sciences*, *112*, 103513.

Panti, C., Cuitiño, J. I., Noetinger, S., Pérez, D., Tapia, M. J., Allende Mosquera, A., Gutiérrez, D. G., Barreda, V. D., & Palazzesi, L. (2025). Tropical seagrasses reached Patagonia during Miocene times. *Communications Earth & Environment*, *6*(1), 564.

Paolucci, F., Buono, M. R., Fernández, M. S., & Cuitiño, J. (2021). Systematic revision of a Miocene sperm whale from Patagonia, Argentina, and the phylogenetic signal of tympano-periotic bones in Physeteroidea. *Acta Palaeontologica Polonica*, *66*(1), 63–76.

Parma, S. G. (2012). El género *Brissopsis* L. Agassiz, 1840 (Echinoidea: Spatangoida) en el Paleógeno y Neógeno de la República Argentina. *Revue de Paléobiologie, Vol. spéc.*, *11*, 417–427.

Parras, A., & Casadío, S. (2006). The oyster *Crassostrea? hatcheri*, a physical ecosystem engineer from the Upper Oligocene–Lower Miocene of Patagonia, Southern Argentina. *Palaios*, *21*(2), 168–186.

Parras, A. M., & Cuitiño, J. I. (2021). Revised chrono and lithostratigraphy for the Oligocene–Miocene Patagoniense marine deposits in Patagonia: implications for stratigraphic cycles, paleogeography, and major drivers. *Journal of South American Earth Sciences*, *110*, 103327.

Parras, A., Dix, G. R., & Griffin, M. (2012). Sr-isotope chronostratigraphy of Paleogene–Neogene marine deposits: Austral Basin, southern Patagonia (Argentina). *Journal of South American Earth Sciences*, *37*, 122–135.

Pastorino, G., & Simone, L. R. L. (2021). Revision of the genus *Buccinanops* (Mollusca: Neogastropoda: Nassariidae), an endemic group of gastropods from the Southwestern Atlantic, including a new genus and accounts on the Buccinanopsinae classification. *Journal of Zoological Systematics and Evolutionary Research*, *59*(6), 1209–1254.

Pérez, D., Alvarez, M., & Santelli, M. B. (2017). Reassessment of *Neovenericor* Rossi de García, Levy & Franchi, 1980 (Bivalvia: Carditidae) using a geometric morphometric approach, and revision of planicostate carditids from Argentina. *Alcheringa*, *41*(1), 112–123.

Pérez, D. E., Farroni, N., Allende Mosquera, A., & Cuitiño, J. I. (2023). First discinid brachiopods (Brachiopoda: Lingulida) from the Cenozoic of Patagonia (Gaiman Formation, Lower Miocene, Argentina). *Ameghiniana*, *60*(3), 203–215.

Pérez, D., Farroni, N., Allende Mosquera, A., & Cuitiño, J. I. (2024). Clusters of *Discinisca messii* (Brachiopoda, Lingulida) en la Formación Puerto Madryn (Mioceno Tardío, Chubut). *Publicación Electrónica de la Asociación Paleontológica Argentina*, *24*(R3), R131.

Pérez, D. E., Cuitiño, J. I., & Soto, I. M. (2025). A new species of *Neovenericor* (Bivalvia: Carditidae) from Patagonia (Gaiman Formation, Argentina) and an evaluation of the presence of *Neovenericor* in the Early Miocene. *Historical Biology*, *38*(1), 8–19. https://doi.org/10.1080/08912963.2025.2472452

Pérez, L. M., Griffin, M., & Manceñido, M. O. (2013). Los macroinvertebrados de la Formación Paraná: Historia y diversidad de la fauna bentónica del Mioceno marino de Entre

Ríos, Argentina. *Asociación Paleontológica Argentina, Publicación Especial*, *14*, 56–70.

Philippi, R. A. (1887). *Los fósiles terciarios i cuartarios de Chile*. Brockhaus.

Pilsbry, H. A. (1929). *Neverita reclusiana* (Desh.) and its allies. *The Nautilus*, *42*(4), 109–113.

Piro, A., & Acosta Hospitaleche, C. (2022). A new petrel (Aves: Procellariidae) from the early Miocene of Patagonia (Argentina). *Historical Biology*, *34*(1), 141–151.

Plotnick, R., & Wagner, P. (2006). Round up the usual suspects: common genera in the fossil record and the nature of wastebasket taxa. *Paleobiology*, *32*(1), 126–146.

Ponder, W. F. (1973). A review of the Australian species of *Penion* Fischer (Neogastropoda: Buccinidae). *Journal of the Malacological Society of Australia*, *2*, 401–428.

Powell, A. W. B. (1951). *Antarctic and subantarctic Mollusca: Pelecypoda and Gastropoda*. Discovery Reports.

Quoy, J. R. C., & Gaimard, J. P. (1833). *Voyage de la corvette l'Astrolabe: exécuté par ordre du roi, pendant les années 1826-1827-1828-1829, sous le commandement de M. J. Dumont d'Urville. Zoologie 2(2).* In J. Dumont d'Urville (Ed.), Voyage de Découvertes de L'Astrolabe (pp. 321–686). J. Tastu, Éditeur-Imprimeur.

Rafinesque, C. (1815). *Analyse de la Nature ou Tableau de l'univers et des corps organisés*. Published by the author.

Reichler, V. A. (2010). Estratigrafía y paleontología del Cenozoico del Gran Bajo del Gualicho y Salinas del Gualicho, Argentina, y descripción de 17 especies nuevas. *Andean Geology*, *37*(1), 177–219.

Reichler, V. A. (2011). *Venericor* (*Neovenericor*) (Mollusca: Bivalvia) en el Mioceno de Patagonia oriental. *Historia Natural, Tercera Serie*, *1*(2), 49–63.

Rochebrune, A. T. de, & Mabille, J. (1885). Diagnoses de mollusques nouveaux, recueillis par les membres de la mission du Cap Horn et M. Lebrun, Préparateur au Muséum, chargé d'une mission à Santa-Cruz de Patagonie. *Bulletin de la Société Philomathique de Paris*, *7*(9), 100–111.

Rojas, A., Zaffaroni, J. C., & Martínez, S. (2018). New molluscan records and palaeoecology of the Late Pleistocene marine assemblage from La Coronilla (Rocha, Uruguay). *Journal of Sedimentary Environments*, *3*(4), 220–233.

Rossi de García, E., Levy, R., & Franchi, M. R. (1980). *Neovenericor* n. gen. (Bivalvia) su presencia en el Miembro Monte León (Formación Patagonia). *Revista de la Asociación Geológica Argentina*, *35*(1), 59–71.

Rossi de García, E., & Levy, R. (1989). Presencia de *Amplaster* sp. nov. (Echinodermata, Clypeasteroidea) en el Terciario de Patagonia. *Actas del 4° Congreso Argentino de Paleontología y Bioestratigrafía* (pp. 89–92). Mendoza.

Sacco, F. (1897). I Molluschi dei terreni terziarii del Piemonte e della Liguria, Parte 23 (Ostreidae, Anomiidae, Dimyidae). *Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di Torino*, *12*(298), 99–100.

Salvini-Plawen, L. (1980). A reconsideration of systematics in the Mollusca (Phylogeny and higher classification). *Malacologia*, *19*(2), 249–278.

Santelli, M. B., & del Río, C. J. (2014). Revisión de la Subfamilia Crassatellinae (Bivalvia: Crassatellidae) del Paleógeno—Neógeno de Argentina. *Ameghiniana*, *51*(4), 311–332.

Saporiti, E. (1938). *Revisión de las especies típicas de* Ostrea *fósiles del Cretáceo superior y Terciario de la República Argentina* [PhD Thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires]. Retrieved from https://hdl.handle.net/20.500.12110/tesis_n0221_Saporiti

Scasso, R. A., & Bellosi, E. S. (2004). Cenozoic continental and marine trace fossils at the Bryn Gwyn paleontological park, Chubut. In R. A. Scasso, & E. S. Bellosi (Eds.), *Bryn Gwyn Guidebook. I International Congress on Ichnology* (pp. 1–19). Trelew.

Scasso, R. A., & Castro, L. N. (1999). Cenozoic phosphatic deposits in North Patagonia, Argentina: Phosphogenesis, sequencestratigraphy and paleoceanography. *Journal of South American Earth Sciences*, *12*(5), 471–487. https://doi.org/10.1016/S0895-9811(99)00035-8

Scasso, R. A., McArthur, J. M., del Río, C. J., Martínez, S., & Thirlwall, M. F. (2001). $^{87}Sr/^{86}Sr$ late Miocene age of fossil molluscs in the "Entrerriense" of the Valdés Peninsula (Chubut, Argentina). *Journal of South American Earth Sciences*, *14*, 319–329.

Schneider, J. A. (2002). Phylogeny of cardiid bivalves (cockles and giant clams): revision of the Cardiinae and the importance of fossils in explaining disjunct biogeographical distributions. *Zoological Journal of the Linnean Society*, *136*, 321–369.

Schumacher, C. F. (1817). *Essai d'un nouveau système des habitations des vers testacés*. Schultz.

Simpson, G. G. (1935). Early and middle Tertiary geology of the Gaiman region, Chubut, Argentina. *American Museum Novitates*, *775*, 1–29.

Smith, E. A. (1875). Descriptions of some new shells from Kerguelen's Island. *Annals and Magazine of Natural History, ser. 4*, *16*(91), 67–73.

Sowerby, G. B. I. (1834). Characters of new species of shells contained in the collection formed by Mr. Cuming, chiefly on the western coast of South America and among the islands of the South Pacific Ocean. *Proceedings of the Zoological Society of London*, *2*, 68–72.

Sowerby, G. B. I. (1846). Description of the Tertiary fossil shells from South America. In C. Darwin (Ed.), *Geological Observations on the volcanic Islands and parts of South America visited during the voyage of H.M.S. "Beagle"* (Appendix, pp. 249–264). D. Appleton and Company.

Sowerby, G. B. II. (1860). Monograph of the genus *Dentalium*. In G. B. Sowerby II (Ed.), *Thesaurus conchyliorum, or monographs of genera of shells* (pp. 97–104). Privately published.

Steinmann, G., & Wilckens, O. (1908). Kreide und Tertiärfossilien aus den Magellansländern, gesammelt von der Schwedischen Expedition 1895–1897. *Arkiv für Zoologi*, *4*, 1–119.

Sterli, J., Vlachos, E., Cuitiño, J., Cerda, I., & Buono, M. (2025). Southernmost dermochelyid turtle from the Miocene. *Ameghiniana*, *62*(4), 1–19.

Stoliczka, F. (1871). *Paleontologica Indica: Cretaceous Fauna of Southern India*. Memoirs of the Geological Survey of India.

Stuardo, J., & Villarroel, M. (1974). On some living and fossil volutes referred to *Miomelon* Dall, 1907 and *Proscaphella* von Ihering, 1907. *The Veliger*, *17*(2), 139–154.

Tambussi, C. P., Degrange, F. J., & de Mendoza, R. S. (2023). "The present state of knowledge of the Cenozoic birds of Argentina" by Tonni 1980: four decades after. *Publicación Electrónica de la Asociación Paleontológica Argentina*, *23*(1), 255–295.

Tryon, G. W. (1862). On the classification and synonymy of the recent species of Pholadidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *14*(5), 191–221.

Viglino, M., Buono, M. R., Gutstein, C., Cozzuol, M. A., & Cuitiño, J. I. (2018). A new dolphin from the early Miocene of Patagonia (Argentina): insights into the evolution of Platanistoidea in the

Southern Hemisphere. *Acta Palaeontologica Polonica*, *63*, 261–277.

Viglino, M., Buono, M. R., Fordyce, R. E., Cuitiño, J. I., & Fitzgerald, E. M. G. (2019). Anatomy and phylogeny of the large shark-toothed dolphin *Phoberodon arctirostris* Cabrera, 1926 (Cetacea, Odontoceti) from the early Miocene of Patagonia (Argentina). *Zoological Journal of the Linnean Society*, *185*(2), 511–542.

Waagen, W. H. (1885). *Salt Range fossils, vol. I, part 4. Productus Limestone fossils, Brachiopoda*. Memoirs of the Geological Survey of India.

Williams, A., Carlson, S., & Brunton, C. (2000). Linguliformea. In R. Kaesler (Ed.), *Treatise on Invertebrate Paleontology, Part H [Brachiopoda (revised), Vol. 2: Linguliformea, Craniiformea, and Rhynchonelliformea (part)]* (pp. H30–H146). Geological Society of America and University of Kansas Press.

Windhausen, A. (1921). Sobre un viaje de reconocimiento geológico a la parte Nordeste del Territorio del Chubut, con referencia especial a la cuestión de la provisión de agua de Puerto Madryn. *Boletín del Ministerio de Agricultura de la Nación. Dirección General de Minas, Geología e Hidrología*, *24*(B), 1–72.

WoRMS Editorial Board. (2025). *World Register of Marine Species*. Available from https://www.marinespecies.org at VLIZ. Accessed 2025-05-06.

Zinsmeister, W. J. (1976). A new genus and species of the gastropod family Struthiolariidae, *Antarctodarwinella ellioti*, from Seymour Island, Antarctica. *The Ohio Journal of Science*, *76*(3), 111–114.

Zinsmeister, W. J., & Camacho, H. H. (1980). Late Eocene Struthiolariidae (Mollusca: Gastropoda) from Seymour Island, Antarctic Peninsula and their significance to the biogeography of early Tertiary shallow-water faunas of the Southern Hemisphere. *Journal of Paleontology*, *54*, 1–14.

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