

Intraspecific variability in the early Miocene struthiolariid gastropod *Perissodonta ameghinoi* (Ihering, 1897) from Tierra del Fuego, Argentina

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INTRASPECIFIC VARIABILITY IN THE EARLY MIOCENE STRUTHIOLARIID GASTROPOD *PERISSODONTA AMEGHINOI* (IHERING, 1897) FROM TIERRA DEL FUEGO, ARGENTINA

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Abstract. The early Miocene marine deposits in Tierra del Fuego bear a group of struthiolariid gastropods that stand out for their high morphological variability. Since the end of the 19th century this variability was interpreted as reflecting (1) a highly diversified rapidly evolving group of species or (2) a single, plastic species characterized by ample intraspecific variability. The morphological study of more than 100 specimens of the Fuegian struthiolariid genus *Perissodonta* Martens collected in the Carmen Silva, Viamonte, and Irigoyen formations indicate that significant parameters, such as shell shape, spire length and number of spiral and axial sculptures (cords, threads, tubercles) vary continuously within an ample range of values, favoring a single, plastic species. Topotype specimens of *Perissodonta ameghinoi* (Ihering), collected from the early Miocene Monte León Formation in Patagonia, show similar plasticity of characters. Furthermore, recent topotype material of *Perissodonta georgiana* Strebel from Islas Georgias del Sur, a species considered very close or junior synonym of the genotype species *P. mirabilis* (Smith), indicates a similar degree of plasticity. Accordingly, the Fuegian struthiolariids previously assigned to *Perissodonta ameghinoi*; *P. fueguina* (Ihering); or *P. densestriata* (Ihering) are here referred to *P. ameghinoi*, a struthiolariid gastropod restricted to the early Miocene in Tierra del Fuego and Patagonia.

Key words. Struthiolariid. *Perissodonta ameghinoi*. Intraspecific variability. Miocene. Tierra del Fuego. Argentina.

Resumen. VARIABILIDAD INTRAESPECÍFICA DEL GASTRÓPODO STRUTHIOLARIDO *PERISSODONTA AMEGHINOI* (IHERING, 1897), MIOCENO TEMPRANO, TIERRA DEL FUEGO, ARGENTINA. Los depósitos marinos del Mioceno temprano en Tierra del Fuego albergan un grupo de gasterópodos struthiolaridos que se destacan por su alta variabilidad morfológica. Desde finales del siglo 19 se interpretó que esta variabilidad reflejaba (1) un grupo de especies altamente diversificado en rápida evolución o (2) una única especie plástica caracterizada por una amplia variabilidad intraespecífica. El estudio morfológico de más de 100 ejemplares del género *Perissodonta* Martens recolectados en las formaciones fueguinas Carmen Silva, Viamonte e Irigoyen indica que parámetros significativos, como la forma del caparazón, la longitud de la espira y el número de ornamentaciones espirales y axiales (líneas espirales finas, cordones, tubérculos) varían continuamente dentro de una amplia gama de valores, favoreciendo una única especie plástica. Los especímenes topotipo de *Perissodonta ameghinoi* (Ihering), recolectados de la Formación Monte León del Mioceno temprano en la Patagonia, muestran una plasticidad de caracteres similar. Además, material de topotipo reciente de *Perissodonta georgiana* Strebel de las Islas Georgias del Sur, una especie considerada sinónimo muy cercano o junior del genotipo de la especie *P. mirabilis* (Smith), indica un grado similar de plasticidad. En consecuencia, los struthiolaridos fueguinos asignados previamente a *Perissodonta ameghinoi*; *P. fueguina* (Ihering) o *P. densestriata* (Ihering) se refieren en este trabajo a *P. ameghinoi*, un gasterópodo struthiolarido restringido al Mioceno temprano en Tierra del Fuego y Patagonia.

Palabras clave. Struthiolaridos. *Perissodonta ameghinoi*. Variabilidad intraespecífica. Mioceno. Tierra del Fuego. Argentina.

MIOCENE MARINE DEPOSITS of Tierra del Fuego bear a group of struthiolariid gastropods that stand out for their high morphological variability, particularly regarding their spiral and axial sculptures, *i.e.*, number and strength of spiral cords, threads, and tubercles. In the struthiolariid material originally described from the South Atlantic coast of Santa Cruz and Tierra del Fuego, this variability was interpreted

as reflecting either (1) a number of different species typifying a highly diversified and rapidly evolving group (*e.g.*, Ihering, 1897, 1907; Ortmann, 1902; Camacho & Zinsmeister, 1989) or (2) a single, plastic species characterized by ample intraspecific variability (*e.g.*, Steinmann & Wilckens, 1908). Both interpretations, however, were generally based on scarce material and limited stratigraphic data, hampering

proper evaluation on the validity of these contrasting views.

The struthiolariid gastropods collected from early Miocene deposits along the Atlantic coast of Santa Cruz and Tierra del Fuego have been generally split into a number of species or varieties, totalizing a number of seven species of *Perissodonta* Martens, 1878, which include *P. ornata* (Sowerby, 1846), *P. ameghinoi* (Ihering, 1897), *P. multinodosa* (Ortmann, 1902), *P. fueguina* (Ihering, 1907), *P. densestriata* (Ihering, 1907), *P. cuevensis* (Camacho & Zinsmeister, 1989), and *P. patagoniensis* (Camacho & Zinsmeister, 1989) (see also Genta Iturrería & Griffin, 2018). In the Atlantic coast of Santa Cruz the first known struthiolariid from Patagonia is *Perissodonta ornata* that was described by Sowerby while studying the material collected by Darwin (1846) from marine deposits of the Monte León Formation, Santa Cruz—see Griffin & Nielsen (2008) and Parras & Griffin (2009) for a detailed stratigraphic account of Darwin's localities and Nielsen (2005) and López Cabrera & Olivero (2018) regarding the generic assignation. Subsequently, Ihering (1897, 1907) studied struthiolariid gastropods from the Monte León (early Miocene) and the San Julián (latest Oligocene–earliest Miocene) formations. Additional struthiolariid species—and varieties subsequently elevated to specific rank—were studied by Ortmann (1902) and Camacho & Zinsmeister (1989). Struthiolariid gastropods from the Monte León Formation were also mentioned and figured by del Río (2002, 2004). Earliest mentions of fossil *Perissodonta* from the Miocene of Tierra del Fuego are from the Carmen Silva Formation (Ihering, 1907; Steinmann & Wilckens, 1908). Additional material from this formation was described by Malumián *et al.* (1978), Camacho & Zinsmeister (1989), López Cabrera & Olivero (2018), and mentioned by Feldmann *et al.* (2011).

Perissodonta is abundant in the early Miocene deposits of Tierra del Fuego and more than 100 specimens have been collected by the authors from five localities, *i.e.*, Sierra Carmen Silva, Punta Basílica, Cerro Águila, Cabo Viamonte, and Río Irigoyen (Fig. 1). Specimens of *Perissodonta* in our collection are characterized by highly variable morphological characters, particularly regarding the shell shape, type and character of the inductura, suture and siphonal canal, and strength and number of spiral cords, spiral threads

and tubercles. As mentioned above, this variability has been interpreted as typifying rapidly evolving different species or intraspecific variation within a single species. Therefore, the purpose of this paper is to review the taxonomy of the *Perissodonta* species from Tierra del Fuego. To accomplish this task, we characterize the morphological variability of a large collection of Fuegian specimens collected from different, but basically coeval stratigraphic units, and the resulting pattern is used to evaluate the paleobiological significance of the variability. Based on these studies, the main conclusion is that most likely the studied material corresponds to a single, highly variable species, which can be accommodated in *Perissodonta ameghinoi*, as Steinmann & Wilckens (1908) and López Cabrera & Olivero (2018) have suggested before.

GEOLOGICAL SETTING

The Upper Cretaceous–Cenozoic sedimentary deposits of Tierra del Fuego integrate the Austral (Magallanes) and part of the Malvinas foreland basins. In central and northern Tierra del Fuego the Río Chico Arch, a structural high of basement rocks, separates the Austral basin from the Malvinas basin. To the south, this structural high disappears and both basins are integrated (Fig. 1; Biddle *et al.*, 1986; Galeazzi, 1998; Olivero *et al.*, 2002; Torres Carbonell & Olivero, 2019). The Austral and Malvinas foreland basins share a geologically similar sedimentary fill, which accumulated synchronously with several contractional stages following a major ductile deformation phase, associated with the closure and inversion of the predecessor Late Jurassic–Early Cretaceous Rocas Verdes back-arc basin (Dalziel, 1981; Torres Carbonell *et al.*, 2020, and the bibliography therein). Within the thrust and fold belt, the Late Cretaceous to Oligocene–earliest Miocene foreland basin fill consists of three unconformity-bounded syntectonic clastic wedges of Late Cretaceous–Danian, Paleocene–early mid Eocene, and late mid Eocene–Oligocene–earliest Miocene age. These clastic wedges accumulated in successive elongated fore-deeps oriented subparallel to the Fuegian Andes (Fig. 1). North of the deformation front, a fourth Miocene clastic wedge consists dominantly of subhorizontal strata included in the Cabo Domingo Group (Malumián & Olivero, 2006; Olivero & Malumián, 2008).

Late Cretaceous to Oligocene–earliest Miocene clastic wedges consist dominantly of thick axial and transverse turbidite systems (Olivero *et al.*, 2003; Torres Carbonell & Olivero, 2012, 2019; Olivero & Torres Carbonell, 2021). The youngest, early Miocene foredeep fill that forms part of the Cabo Domingo Group consists also of axial and transverse turbidite systems, including spectacular channel-levee

complexes and canyon-gully deposits of the Viamonte Formation (Olivero & Torres Carbonell, 2021). Within the thrust and fold belt, in the Río Irigoyen area, near the trace at the Atlantic coast of the major Magallanes-Fagnano transform fault (Torres Carbonell *et al.*, 2008, 2011), faulted blocks of coarse conglomerate, sandstone and mudstone of the Irigoyen Formation were partly referred to the Pliocene

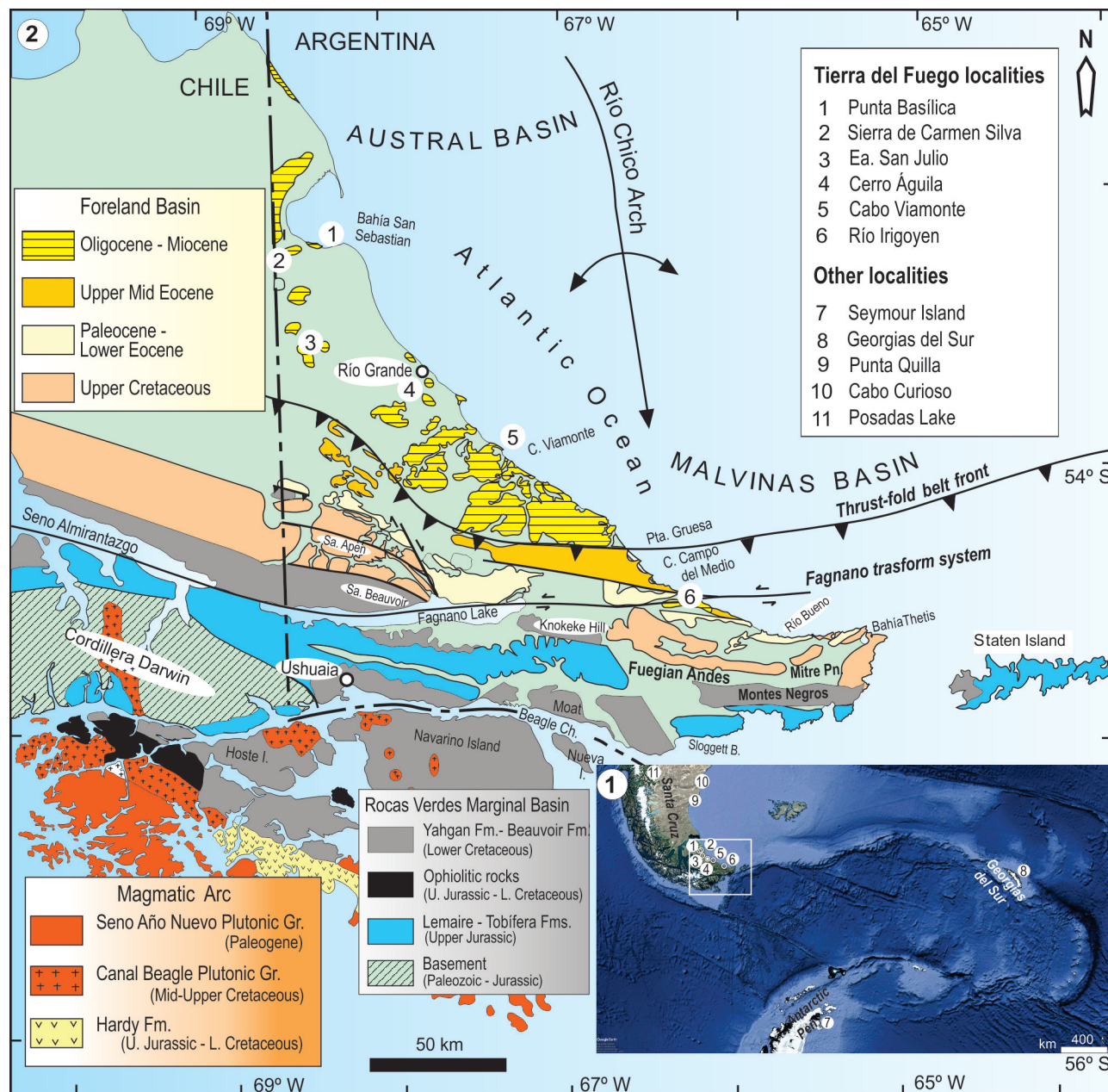


Figure 1.1. Location map showing provenance of the studied material from Tierra del Fuego (1 to 6) and of the material used for comparison (7 to 11) from Antarctica (Seymour Island), Georgias del Sur, and Santa Cruz Province. 2, Geological sketch map of Tierra del Fuego with location of the studied material.

(Malumián & Olivero, 2005). The geology and age of the Irigoyen Formation, however, are not well defined. It is probably of early Miocene age according to the calcareous nannoplankton content (Bedoya-Agudelo, 2019). Besides, the foraminiferal assemblage of the Irigoyen Formation is very similar to the Carmen Silva Formation (*cf.* Malumián & Olivero, 2005), the age of which is now interpreted as early Miocene (see Olivero & Torres Carbonell, 2021). The rest of the Cabo Domingo Group exposed in northern and western Tierra del Fuego (Fig. 1), includes shallow marine deltaic deposits of the early Miocene Carmen Silva Formation (Codignotto & Malumián, 1981; Torres Carbonell & Olivero, 2019; Olivero & López Cabrera, 2020), continental deposits of the Miocene Castillo Formation (Codignotto & Malumián, 1981; Malumián & Olivero, 2006) and fluvial deposits of the late early Miocene Cullen Formation (Olivero *et al.*, 2015; Olivero & Torres Carbonell, 2021).

The studied fossil material of the gastropod genus *Perissodonta* was all recovered from different localities and formations of the Cabo Domingo Group (Figs. 1, 2). Most of the collection comes from different stratigraphic horizons of Carmen Silva Formation exposed in the Sierra Carmen Silva, Estancia San Julio, and Punta Basílica. The rest of the material was collected at several localities from exposures of Viamonte and Irigoyen formations (see the section “*Perissodonta* fossil-bearing localities”).

MATERIAL AND METHODS

The database for this study consists of gastropod specimens collected by the authors during several summer field seasons between the years 2004 and 2020 in Antarctica, Patagonia (Santa Cruz Province), and Tierra del Fuego. The material from Tierra del Fuego under study is compared with fossil species of *Perissodonta* from Miocene deposits of Santa Cruz Province, as well as with extant species of *Perissodonta georgiana* Strebel, 1908 from Georgias del Sur, both housed in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina. Additional material collected by the authors in the classical localities of the latest Oligocene–earliest Miocene San Julián Formation in the Atlantic coast of Santa Cruz Province (Cabo Curioso, Playa La Mina), the early Miocene Monte León Formation near the towns of Coman-

dante Piedrabuena and Puerto Santa Cruz (Punta Quilla at the mouth of the Río Santa Cruz and Mount Entrance) and from the early Miocene El Chacay Formation, near Lago Posadas, were used for comparison with the *Perissodonta* material from Tierra del Fuego (Fig. 1). However, only the well-preserved material from the Monte León Formation (Piedrabuena and Río Santa Cruz mouth) was included in the morphological analysis. The material from the San Julián and El Chacay formations is incomplete or deformed by lateral compression, thus it is not suitable for measurements. Even though, the El Chacay struthiolariids bear a general resemblance to *P. ameghinoi* they were not included in the morphological analysis. A large collection of *Perissodonta* (= *Struthiolarella*) and *Antarctodarwinella* Zinsmeister, 1976 collected by one of the authors (EBO) from the late mid Eocene to late Eocene La Meseta Formation, Seymour Island, Antarctica was also available for comparison with the Miocene material.

For the study of the variability in *Perissodonta* we follow the approaches used by most of the researchers that have studied fossil species of this genus. In addition to the format used by Ihering (1897, 1907) and Ortmann (1902), we follow in particular the one used by Steinmann & Wilkens (1908) and Camacho & Zinsmeister (1989) to group and analyze morphological characters of the shell of *Perissodonta*. This procedure has proven useful to compare the species and variation of morphological characters described in these studies with our material. Basically, used morphological terms and measurements include: shell height (H); shell width (W); spire height (Sh); last whorl height (Lwh); proportion between Sh and H, defined as $100 \cdot \text{Sh}/\text{H}$; number and strength of spiral cords, spiral threads, and tubercles (see Fig. 3.1).

The studied material is housed at the paleontological collections of the Centro Austral de Investigaciones Científicas (CADIC-CONICET), Ushuaia, Argentina, under the numbers CADIC PI 610–623. The material housed at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires is identified with the acronyms MACN-Pi 763 and MACN-In 36298, 18955, 18953.

PERISSODONTA FOSSIL-BEARING LOCALITIES IN TIERRA DEL FUEGO

Carmen Silva Formation

In the Carmen Silva Formation, fossiliferous beds with *Perissodonta* are recorded in both the Sierra Carmen Silva beds and the Punta Basílica beds. These beds are interpreted as distinct coarsening upwards delta successions (Torres Carbonell & Olivero, 2019) and were differentiated as informal units of the Carmen Silva Formation by Olivero & López Cabrera (2020).

Sierra de Carmen Silva beds. These beds include two fossil localities. At one locality the studied fossils come from the upper part of the prodelta mudstones exposed in the Sierra de Carmen Silva, just east of the Chilean-Argentinean border (Fig. 1, locality 2, point 135: 53° 19' 38.1" S, 68° 35' 32" W; see Torres Carbonell & Olivero, 2019). At this locality *Perissodonta ameghinoi* is associated with abundant specimens of the genus *Turritella* Lamarck, 1799 (Fig. 2.1). The two species are represented by well-preserved shells dispersed in mudstone, with no sign of reworking or reorientation by currents, and are interpreted as an autochthonous association. At the second locality the specimens lie in cross-stratified conglomerate, coarse-grained sandstones and pebbly sandstones exposed in quarries and artificial cuts along the road to Estancia San Julio (Fig. 1, locality 3. Point 545: 53° 38' 40" S, 68° 22' 27" W; Point 690: 53° 39' 51.2" S, 68° 29' 6.8" W). These coarse-grained beds probably represent proximal prodelta and distributary mouth bars (cf. Feldmann *et al.*, 2011; Torres Carbonell & Olivero, 2019). Shell reworking by currents is evident and *Perissodonta* forms part of a para-autochthonous-allochthonous mixture of partially broken or relatively complete shells, commonly concentrated together with bivalves, gastropods and crustacean decapods in lenses within the conglomerate and coarse-grained sandstones (Fig. 2.2).

Punta Basílica beds. These beds includes fossil gastropods such as the relatively abundant *Turritella* sp., *Perissodonta ameghinoi*, specimens of the bivalve genus *Barnea* Risso, 1826 in life position, crustacean decapods, barnacles, solitary corals and leaves of *Nothofagus*. Fossils are generally well-preserved in fine-grained silty sandstone and fine- to medium-grained sandstone or else are represented by scattered and partially broken shells concentrated in fine-grained

conglomerate (Fig. 1; locality 1 (PB 731), 53° 18' 10" S, 68° 24' 48.9" W). Fossiliferous beds form part of steeply inclined delta-front clinoform deposits (Fig. 2.3–4). In particular, the stratigraphically older clinoform deposits record wave ripples and wave-ripple cross-lamination and cross-stratified sandstones forming large compound dunes and tidal bars (Olivero & López Cabrera, 2020).

Viamonte Formation

Fossil mollusks, including *Perissodonta ameghinoi*, are recorded in two of the main architectural elements (Fig. 2.5–7) of the deep-water turbidite systems recognized in the Viamonte Formation (see Olivero & Torres Carbonell, 2021). In the transverse turbidite system *Perissodonta*, other gastropods, bivalves, corals, barnacles, and crustacean decapods are recorded in fine-grained conglomerates forming part of the element gullies and other slope deposits of this system. In the axial turbidite system *Perissodonta*—commonly associated with dense concentration of *Turritella* sp.—is recorded also in heterolithic slumped beds and fine-grained debris flows, at the base of the architectural element channel belt of this system (Olivero & Torres Carbonell, 2021). In both architectural elements, the lithology is well-cemented and very hard, rendering impossible the recovery of fossil material adequate for measurement. Only field photographs (Fig. 2.6–7) and a few internal molds or broken specimens (Locality 5, point 164 54° 02' 32.5" S, 67° 19' 39.9" W) are available.

Additional specimens of *Perissodonta ameghinoi* were also recorded in the Cerro Águila conglomerate in association with bivalves, other gastropods, solitary corals, and crustacean decapods (Locality 4, 53° 50' 11.15" S, 67° 47' 31.85" W). The stratigraphic relationship of the Cerro Águila channelized conglomerates is not clear, but together with the Cabo Peñas conglomerates it probably forms part of the transverse turbidite system of the Viamonte Formation (cf. Olivero & Torres Carbonell, 2021).

Irigoyen Formation

The ichnology and sedimentology of the shallow-marine deposits of the Irigoyen Formation are presently under study by the authors. However, they can be generally characterized as inner shelf deposits (Malumián & Olivero, 2005)

that reach a minimum thickness of *ca.* 65 m. The lower part, including a thick, slumped horizon with abundant reworked carbonized logs, gastropods, bivalves and corals originated below wave and tidal influence. This horizon is covered in onlap relationship by parallel-laminated and cross-bedded fine-grained sandstone beds that grade upwards to silty very fine-grained bioturbated sandstones and to cross-stratified sandstones defining shallow channels. The top of the succession is marked by fossiliferous, cross-stratified channelized conglomerates (Fig. 2.8). The gastropod *Perissodonta* is relatively abundant in the basal slump horizon and in the upper channelized conglomerate (Fig. 1; locality 6, points 841, 845, 54° 30' 37.2" S, 66° 17' 55.5" W).

THE RECORD OF MIOCENE *PERISSODONTA* IN PATAGONIA AND TIERRA DEL FUEGO

Since their earliest mention in the mid-19th century, struthiolariid gastropods from the Cenozoic of Patagonia, Tierra del Fuego and Georgias del Sur were initially included in the genus *Struthiolaria* Lamarck, 1816 and later in *Struthiolarella* Steinmann & Wilckens, 1908, but presently these struthiolariids are assigned to the genus *Perissodonta* (see Systematic Paleontology). The first known struthiolariid from Patagonia is *Perissodonta ornata*, that was described by Sowerby while studying the material collected by Darwin (1846) from marine deposits of the Monte León Formation, Santa Cruz (see Griffin & Nielsen, 2008). The diagnosis of *P. ornata* includes a canaliculated suture and two (rarely three) strong cords in the last whorl. These last two characters and the small size of the specimen are very distinctive and characteristic of *P. ornata* (personal observation of the authors in the type locality). Philippi (1887) erected *Perissodonta chilensis* (Philippi, 1887) from Matanzas, Navidad (Chile), based on the nodular aspect of the tubercles and five or six spiral cords in the last whorl (see also Nielsen, 2005). Ihering (1897), studying specimens of "*Struthiolaria*" from the Monte León Formation erected *Perissodonta ameghinoi*. Its original diagnostic characters included 15 sharp tubercles, eight or nine narrow spiral threads, and five or six spiral cords in the last whorl. He also noted the close similarities in ornamentation shared by *P. chilensis* and *P. ameghinoi*. Additional species and varieties subsequently elevated to the specific rank were established by Ortmann (1902) and

Camacho & Zinsmeister (1989) from the Miocene of Santa Cruz Province. These include *Perissodonta multinodosa*, *Perissodonta cuevensis*, and *Perissodonta patagoniensis*. The latter, however, is considered herein as a synonym of *P. ornata* due to its characteristic canaliculated suture and two strong cords. Ortmann (1902) also erected *Perissodonta hatcheri* from Eocene deposits of Punta Arenas, Chile, which carries spiral cords equally developed all over the shell surface, a character by which it differs from the rest of the species of *Perissodonta*.

Earliest mentions of fossil *Perissodonta* from Tierra del Fuego are from the Carmen Silva Formation and correspond to *P. fueguina* (cf. Camacho & Zinsmeister, 1989) and *P. ameghinoi* described by Steinmann & Wilckens (1908). The latter was designated the type species of the newly erected genus *Struthiolarella*, but the genus is now considered a junior synonym of *Perissodonta* (see Systematic Paleontology). Malumián *et al.* (1978) recorded *Perissodonta densestriata* from the locality of Estancia La Federica (Carmen Silva Formation) and Camacho & Zinsmeister (1989) reported *P. fueguina* from the same locality.

The material from Tierra del Fuego assigned to *P. ameghinoi* by Steinmann & Wilckens (1908) included four specimens, collected from outcrops located in the northern part of the island named Sierra de Carmen Silva, Barranca de Carmen Silva or San Sebastián (*i.e.*, Punta Basílica), and the Atlantic coast between Punta Sinai and Cabo Domingo. They stressed the strong variability of the spiral sculpture, the height of the spire, and characters of the aperture and callus. Interestingly, Steinmann & Wilckens (1908) included the extant *Perissodonta mirabilis* (Smith, 1875) from Kerguelen, as a synonym of the new genus *Struthiolarella* not noticing, however, that *S. mirabilis* is the type species of the genus *Perissodonta* (cf. Powell, 1951; Griffin & Nielsen, 2008; López Cabrera & Olivero, 2018).

Species described so far from Patagonia show also a large variability of the shell morphology, such as spire height and number of threads, cords and tubercles. The material described by Ortmann (1902) and Ihering (1897, 1907) was compiled by Camacho & Zinsmeister (1989) in a systematic study. Although in that study they show intermediate forms in some species, such as *P. ameghinoi* and *P. multinodosa*, particularly regarding the intergradation in the number and

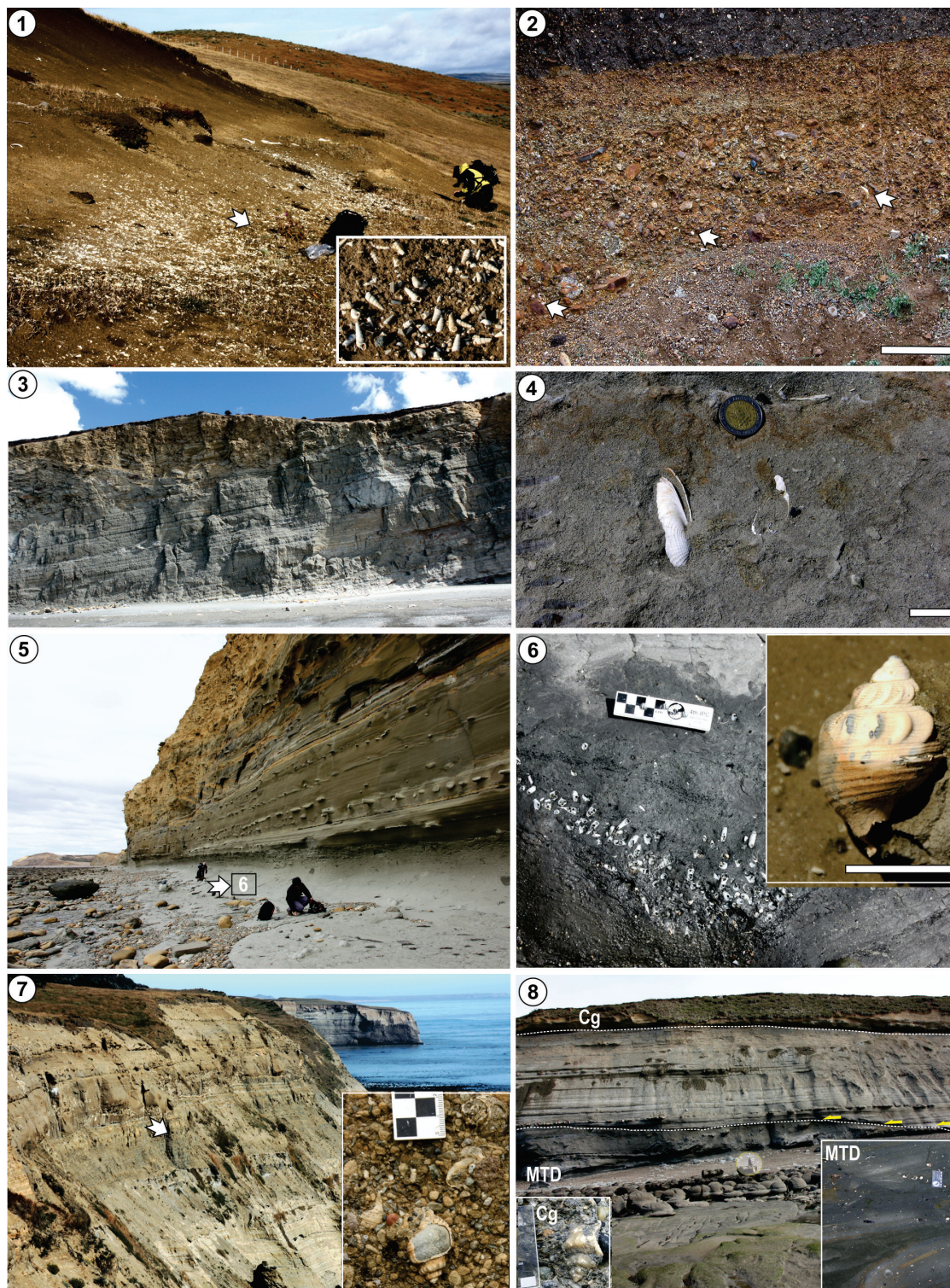


Figure 2. Localities with the studied *Perissodonta ameghinoi* from Tierra del Fuego. 1–4, Carmen Silva Formation. 1, Sierra Carmen Silva, locality 2, point 135, with abundant gastropods (inset) in some horizons (white arrow); 2, Quarry near Estancia San Julio, locality 3, point 545, scale bar 40 cm; 3, Punta Basílica beds, locality 1, point PB 731, height of cliff c. 20 m, with fossiliferous horizons; 4, note *Barnea* sp. in living position, scale bar 2 cm. 5–7, Viamonte Formation. 5–6, locality 5, point 164, channel-levee system of the axial channel belt (5), preserving abundant turritellids and *Perissodonta ameghinoi* (inset in 6, scale bar 1 cm) in slumped, heterolithic blocks and debris flow deposits (6); 7, gully and slope facies of the transverse system, with fossiliferous conglomerates (arrow) with *Perissodonta ameghinoi* (inset). 8, Irigoyen Formation, locality 6, points 841, 845, note large mass transport deposit (MTD) covered in onlap relationship (yellow arrows) by fine-grained silty sandstones and mudstones, and coarse-grained conglomerate (Cg) on top of the cliff, circled person for scale. The MTD and conglomerate both preserve *Perissodonta ameghinoi* (insets, scale in cm).

shape of tubercles, they used these characters to differentiate the species. The study of intraspecific variability in the species of *Perissodonta* restricted to Santa Cruz is beyond the scope of this study. Instead, we restrict our study to the analysis of the variability in the *Perissodonta* species so far mentioned or described from Tierra del Fuego, which includes *P. ameghinoi*, *P. fueguina*, and *P. densestriata*, which we suggest can be reunited in the single, plastic species *P. ameghinoi*.

MORPHOLOGICAL VARIABILITY IN THE FUEGIAN *PERISSODONTA*

The general morphology of *Perissodonta* specimens from Tierra del Fuego is characterized by medium to large size, globose (W/H: 0.9) to sub-globose (W/H: 0.6) shells with a convex to squarish or scalariform outline; highly variable proportion between Sh and H (average 33.0%, range 10.1–49.5%); sub-oval shell aperture, widening adapically; inner lip with thick inductura; short siphonal canal; and impressed suture. The sculpture of the shell consists of strong spiral cords in the last whorl; narrow spiral threads are present in the adapical part of the whorl; and prosocline tubercles.

To study the variability of the shell morphology in *Perissodonta* we found useful the representation of the ratios between: 1) the spire height (Sh) and the total shell length (H), thus the ratio Sh/H is a measure of the relative height of the spire, and 2) between the shell width (W) and the last whorl height (Lwh), thus the ratio W/Lwh measures the relative width of the shell. In the studied material of *P. ameghinoi* from Tierra del Fuego and Santa Cruz, the ratio Sh/H varies within 0.5 and 0.1, mean value 0.3, whereas the ratio W/Lwh varies between 1.2 and 0.7, mean value 1.0 (Tab. 1). The plot of these ratios shows the total morphospace covered by the studied gastropods, which varies from relatively high spire-wide shells to the right, to relatively low spire-narrow shells to the left (Fig. 3.1). Other plots depict the variability of the shell shape, using the parameters H and W (Fig. 3.2), and the sculpture, plotting the number of cords, threads, and tubercles at different shell heights (Fig. 3.3). These plots (Fig. 3.2–3) include *Perissodonta ameghinoi* from different formations in Tierra del Fuego, as well as *P. ameghinoi* and *P. ornata* from the Monte León Formation, Santa Cruz Province.

In *P. ameghinoi* from Tierra del Fuego and Santa Cruz, the set of parameters used to characterize the morphology varies continuously, showing no distinct clusters in the proportions of the spire height relative to total shell height (Sh/H), or in the maximum shell width relative to the last whorl height (W/Lwh; Fig. 3.1). The same pattern is shown by the plot of the shell length and width (Fig. 3.2). A similar lack of distinct clusters in *P. ameghinoi* from Tierra del Fuego and Santa Cruz is seen in the plot of sculptural characters, including spiral cords, spiral threads, and number of tubercles (Fig. 3.3). Conversely, the morphological and sculptural parameters of *P. ornata* show a distinct cluster of points that clearly separates this species from *P. ameghinoi* (Fig. 3.2).

In order to better illustrate the range of variability in the *Perissodonta* specimens from Tierra del Fuego we have chosen eight representative morphological variants, which were selected according to their characteristic morphological and ornamental characters. These eight morphological variants (Fig. 4–5) are distinguished by a blue square in the plot of Figure 3 and their distinguishing characters are briefly described below.

Morphological variant 1

Shell sub-globose, consisting of six whorls characterized by a squarish outline. Dimensions are 37.9 mm height, 29 mm width, and spire reaching 36% of total height. Thirteen spiral threads, shoulder of the sutural ramp coronate with 12–13 pointed tubercles. The last whorl bears five to six spiral cords followed by seven to eight spiral threads up to the fasciole (Fig. 4.1–3).

Morphological variant 2

The shell is sub-globose, proportionally less wide than morphological variant 1, whorls are slightly squarish in outline. Dimensions are 44 mm height, 25 mm width, and spire reaching 39% of the total height. Thirteen spiral threads, shoulder of the sutural ramp coronate with 14 slightly pointed tubercles. The last whorl bears five spiral cords of equal size followed by seven spiral threads up to the aperture and over the fasciole (Fig. 4.4).

Morphological variant 3

The shell is globose, whorls are convex in outline.

TABLE 1 - Measurements of studied specimens of *Perissodonta* from different localities. CADIC-PI is the inventory number of CADIC collection, and ID is the number identifying a particular specimen

Perissodonta ameghinoi from Tierra del Fuego

CADIC PI	ID	H	W	Bwh	Sh	% spire	W/Bwh	Sh/H	W/H	Sh/Bwh	Cords	Threads	Tubercles	Locality
610	1	39.1	25.6	29.1	10.0	25.6	0.9	0.3	0.7	0.3	7.0	13.0	12.0	690
610	2	38.8	25.0	25.4	13.4	34.5	1.0	0.3	0.6	0.5	4.0	12.0	13.0	690
610	3	52.0	34.5	41.0	11.0	21.2	0.8	0.2	0.7	0.3	5.0	12.0	13.0	690
610	12	35.3	24.2	23.5	11.8	33.4	1.0	0.3	0.7	0.5	7.0	13.0	12.0	690
610	13	44.1	35.0	32.5	11.6	26.3	1.1	0.3	0.8	0.4	6.0	13.0	12.0	690
610	14	36.6	27.2	25.1	11.5	31.4	1.1	0.3	0.7	0.5	7.0	13.0	12.0	690
610	15	44.2	34.0	37.5	6.7	15.2	0.9	0.2	0.8	0.2	5.0	13.0	12.0	690
610	19	37.7	27.3	24.2	13.5	35.8	1.1	0.4	0.7	0.6	6.0	12.0	12.0	690
610	26	35.9	23.2	22.3	13.6	37.9	1.0	0.4	0.6	0.6	6.0	12.0	12.0	690
610	30	42.7	37.0	31.0	11.7	27.4	1.2	0.3	0.9	0.4	5.0	12.0	12.0	690
610	35	34.2	25.8	29.9	4.3	12.6	0.9	0.1	0.8	0.1	5.0	12.0	12.0	690
610	39	32.7	24.6	29.4	3.3	10.1	0.8	0.1	0.8	0.1	7.0	13.0	12.0	690
610	33	43.7	32.2	29.7	14.0	32.0	1.1	0.3	0.7	0.5	5.0	13.0	12.0	690
611	6	38.3	25.2	24.6	13.7	35.8	1.0	0.4	0.7	0.6	7.0	13.0	13.0	545
611	4	36.4	23.5	21.3	15.1	41.5	1.1	0.4	0.6	0.7	7.0	12.0	12.0	545
611	8	36.8	25.7	25.7	11.1	30.2	1.0	0.3	0.7	0.4	5.0		12.0	545
611	9	47.6	34.7	32.9	14.7	30.9	1.1	0.3	0.7	0.4	6.0		13.0	545
611	10	33.1	21.1	21.6	11.5	34.7	1.0	0.3	0.6	0.5	7.0	13.0	13.0	545
611	11	37.5	22.4	21.2	16.3	43.5	1.1	0.4	0.6	0.8	6.0	13.0	13.0	545
611	16	40.0	24.4	33.1	6.9	17.3	0.7	0.2	0.6	0.2	6.0	13.0	13.0	545
611	17	43.5	28.2	27.2	16.3	37.5	1.1	0.4	0.7	0.6	5.0	13.0	13.0	545
611	18	42.0	24.8	25.9	16.1	38.3	1.0	0.4	0.6	0.6	5.0	12.0	12.0	545
611	20	43.4	28.9	30.0	13.4	30.9	1.0	0.3	0.7	0.4	7.0	13.0	12.0	545
611	21	38.2	28.9	24.9	13.3	34.8	1.2	0.3	0.8	0.5	6.0	13.0	12.0	545
611	22	42.2	32.7	29.3	12.9	30.6	1.1	0.3	0.8	0.4	6.0	13.0	12.0	545
611	23	43.8	29.9	35.4	8.4	19.2	0.8	0.2	0.7	0.2	7.0	13.0	13.0	545
611	24	42.5	27.4	28.1	14.4	33.9	1.0	0.3	0.6	0.5	6.0	13.0	12.0	545
611	25	41.5	27.4	29.9	11.6	28.0	0.9	0.3	0.7	0.4	6.0	10.0	12.0	545
611	28	37.3	23.7	24.5	12.8	34.3	1.0	0.3	0.6	0.5	6.0	12.0	12.0	545
611	29	35.4	22.0	22.1	13.3	37.6	1.0	0.4	0.6	0.6	6.0	13.0	12.0	545
611	31	46.6	31.0	32.0	14.6	31.3	1.0	0.3	0.7	0.5	7.0	12.0	12.0	545
611	32	32.0	19.8	19.8	12.2	38.1	1.0	0.4	0.6	0.6	6.0	10.0	12.0	545
611	34	48.0	27.2	28.0	20.0	41.7	1.0	0.4	0.6	0.7	7.0	10.0	12.0	545
611	36	42.2	27.3	28.3	13.9	32.9	1.0	0.3	0.6	0.5	5.0		13.0	545
611	38	37.4	24.4	23.6	13.8	36.9	1.0	0.4	0.7	0.6	6.0	11.0	12.0	545
611	40	31.6	23.9	25.5	6.1	19.3	0.9	0.2	0.8	0.2	6.0	12.0	12.0	545
611	41	47.9	28.8	37.0	10.9	22.8	0.8	0.2	0.6	0.3	6.0	13.0	12.0	545
611	42	38.6	26.2	24.4	14.2	36.8	1.1	0.4	0.7	0.6	6.0	12.0	12.0	545
611	43	48.3	27.0	24.4	23.9	49.5	1.1	0.5	0.6	1.0	6.0	9.0	12.0	545
611	44	44.1	29.4	27.2	16.9	38.3	1.1	0.4	0.7	0.6	6.0	13.0		545
611	46	32.2	20.1	22.2	10.0	31.1	0.9	0.3	0.6	0.5	6.0	12.0	12.0	545
611	47	28.8	19.3	17.5	11.3	39.2	1.1	0.4	0.7	0.6	5.0	9.0	12.0	545
611	48	27.9	20.9	17.2	10.7	38.4	1.2	0.4	0.7	0.6				545
611	49	33.6	20.9	21.6	12.0	35.7	1.0	0.4	0.6	0.6	6.0		12.0	545
611	50	38.3	24.5	23.5	14.8	38.6	1.0	0.4	0.6	0.6	6.0	13.0	12.0	545
611	51	38.4	24.9	24.1	14.3	37.2	1.0	0.4	0.6	0.6	5.0	10.0	12.0	545
611	52	40.4	25.5	25.5	14.9	36.9	1.0	0.4	0.6	0.6	6.0	9.0	13.0	545
611	53	42.5	27.9	27.9	14.6	34.4	1.0	0.3	0.7	0.5	6.0	12.0	12.0	545

TABLE 1 - Continuation

Perissodonta ameghinoi from Tierra del Fuego

CADIC PI	ID	H	W	Bwh	Sh	% spire	W/Bwh	Sh/H	W/H	Sh/Bwh	Cords	Threads	Tubercles	Locality
611	54	37.5	25.7	25.5	12.0	32.0	1.0	0.3	0.7	0.5	6.0	9.0	13.0	545
611	55	39.4	27.2	25.5	13.9	35.3	1.1	0.4	0.7	0.5	6.0	12.0	13.0	545
611	56	38.7	24.1	25.9	12.8	33.1	0.9	0.3	0.6	0.5	5.0	9.0	12.0	545
611	57	37.9	25.2	24.9	13.0	34.3	1.0	0.3	0.7	0.5	6.0		12.0	545
611	58	39.1	25.8	24.7	14.4	36.8	1.0	0.4	0.7	0.6	6.0	9.0	12.0	545
611	59	39.6	26.5	26.2	13.4	33.8	1.0	0.3	0.7	0.5	5.0	10.0	12.0	545
611	60	35.3	25.9	23.9	11.4	32.3	1.1	0.3	0.7	0.5	6.0	9.0	12.0	545
611	61	41.1	27.6	27.9	13.2	32.1	1.0	0.3	0.7	0.5	6.0	9.0	12.0	545
611	62	37.6	25.9	24.8	12.8	34.0	1.0	0.3	0.7	0.5	6.0	12.0	12.0	545
611	63	37.4	26.7	23.9	13.5	36.1	1.1	0.4	0.7	0.6	6.0		12.0	545
611	64	45.9	31.7	29.8	16.1	35.1	1.1	0.4	0.7	0.5	5.0	10.0	12.0	545
611	65	35.9	26.1	23.6	12.3	34.3	1.1	0.3	0.7	0.5	5.0	12.0	12.0	545
611	66	35.3	24.3	23.1	12.2	34.6	1.1	0.3	0.7	0.5	5.0		12.0	545
611	67	35.9	24.3	25.0	10.9	30.4	1.0	0.3	0.7	0.4	6.0	12.0	12.0	545
611	69	41.6	25.4	27.9	13.7	32.9	0.9	0.3	0.6	0.5	6.0	10.0	12.0	545
611	68	34.1	23.6	22.9	11.2	32.8	1.0	0.3	0.7	0.5	6.0	12.0	13.0	545
611	290	41.6	25.5	28.1	13.5	32.5	0.9	0.3	0.6	0.5	6.0	13.0	12.0	545
612	5	42.3	29.0	24.0	18.3	43.3	1.2	0.4	0.7	0.8	7.0	12.0	12.0	PB
612	27	47.0	35.0	29.2	17.8	37.9	1.2	0.4	0.7	0.6	7.0	12.0	12.0	PB
612	7	41.0	31.0	26.2	14.8	36.1	1.2	0.4	0.8	0.6	5.0	13.0	13.0	PB
613	841	21.7	15.9	15.4	6.3	29	1	0.3	0.7	0.4	6.0	13.0		RI
613	RI	28.5	17.7	15.9	12.6	44.2	1.1	0.4	0.6	0.8	6.0	13.0	12.0	RI
614	45	37.5	23.1	24.1	13.4	35.7	1.0	0.4	0.6	0.6	6.0	9.0	12.0	CAG
615	70	35.6	21.1	23.1	12.5	35.1	0.9	0.4	0.6	0.5	6.0	12.0	12.0	135
615	71	34.5	21.6	22.5	12.0	34.8	1.0	0.3	0.6	0.5	6.0	9.0	13.0	135
615	72	35.6	22.2	23.9	11.7	32.9	0.9	0.3	0.6	0.5	6.0	9.0	12.0	135
615	73	32.5	22.7	21.2	11.3	34.8	1.1	0.3	0.7	0.5	7.0	12.0	12.0	135
615	74	33.3	22.2	21.1	12.2	36.6	1.1	0.4	0.7	0.6	6.0	12.0	12.0	135
615	75	33.1	21.4	21.6	11.5	34.7	1.0	0.3	0.6	0.5	7.0		12.0	135
615	76	34.4	23.9	21.6	12.8	37.2	1.1	0.4	0.7	0.6	6.0	12.0	12.0	135
616	77	20.2	13.2	16.4	3.8	18.8	0.8	0.2	0.7	0.2	6.0		12.0	164
Mean		38.4	25.9	25.8	12.7	33.9	1.0	0.3	0.7	0.5	5.9	11.6	12.2	

P. ameghinoi from Santa Cruz. Monte Entrance

CADIC PI	ID	H	W	Bwh	Sh	% spire	W/Bwh	Sh/H	W/H	Sh/Bwh	Cords	Threads	Tubercles	Locality
617	1	53.1	25.1	28.1	25.0	47.1	0.9	0.5	0.5	0.9	5.0	9.0	12.0	E21
617	2	47.2	26.6	27.4	19.8	41.9	1.0	0.4	0.6	0.7	6.0	9.0	18.0	E21
617	3	41.6	25.5	25.8	15.8	38.0	1.0	0.4	0.6	0.6	5.0	9.0	15.0	E21
617	4	44.4	25.5	27.8	16.6	37.4	0.9	0.4	0.6	0.6	5.0	9.0	12.0	E21
617	5	42.4	23.6	25.1	17.3	40.8	0.9	0.4	0.6	0.7	5.0	9.0	12.0	E21
617	6	58.8	34.4	33.7	25.1	42.7	1.0	0.4	0.6	0.7	5.0	9.0	18.0	E21
Mean		47.9	26.8	28.0	19.9	41.3	1.0	0.4	0.6	0.7	5.2	9.0	14.5	

P. ornata from Piedrabuena and Monte Entrance

CADIC PI	ID	H	W	Bwh	Sh	% spire	W/Bwh	Sh/H	W/H	Sh/Bwh	Cords	Threads	Tubercles	Locality
618	1.0	22.7	9.6	13.1	9.6	42.3	0.7	0.5	0.5	0.9	2.0	9.0	12.0	R3 1
618	2.0	18.7	7.5	11.2	7.5	40.1	0.7	0.4		0.6	2.0	9.0	12.0	R3 2
618	6.0	25.0	11.0						0.4		2.0	12.0	18.0	*
Mean		22.1	9.4	12.2	8.6	41.2	0.7	0.4	0.5	0.8	2.0	10.0	14.0	

* *Perissodonta patagoniensis* in Camacho & Zinsmeister (1989)

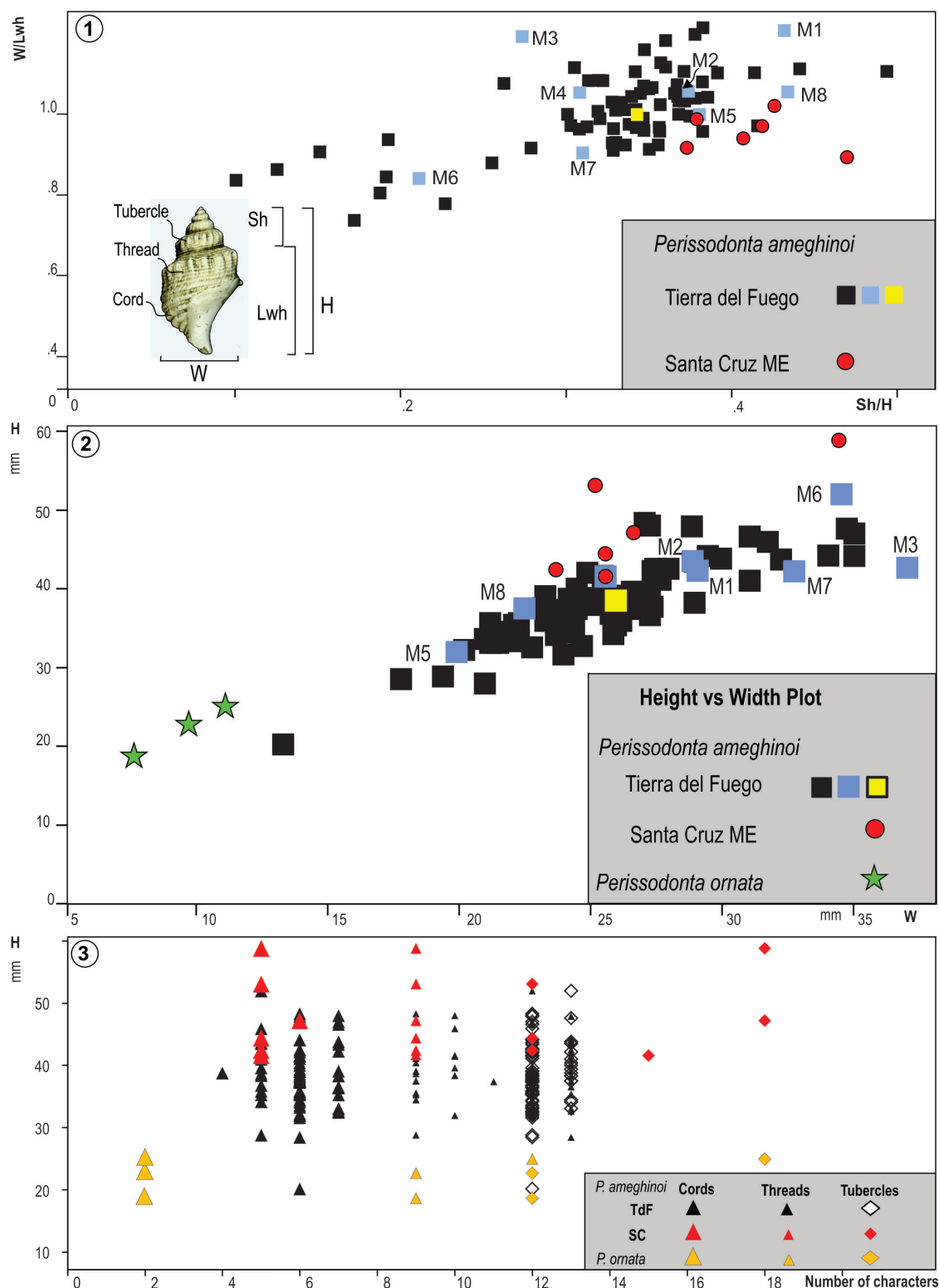


Figure 3. Plot of morphological characters in *Perissodonta*. 1, plot of the ratios W/Lwh and Sh/H in *P. ameghinoides* from Tierra del Fuego (squares) and Mount Entrance, Santa Cruz (red circles). Color fill of squares represents values of actual specimens (black), the mean value (yellow), and representative values for indicated morphological variants (M) (light blue). Note continuity and superposition of the ratios in *P. ameghinoides* specimens from Tierra del Fuego and Santa Cruz, suggesting ample intraspecific variability. Inset indicates the meaning of W , Lwh , H , Sh , and ornamental characters. 2–3, combined plot of H vs. W (B) and H vs. the number (C) of various ornamental characters (cords, threads, and tubercles) in *P. ameghinoides* and *P. ornata*, the latter includes *P. patagoniensis* of Camacho & Zinsmeister (1989). Note that only *P. ornata* occupies a distinct morphospace in both 2 and 3 plots, See text for further explanation.

Dimensions are height 42.4 mm, width 25.6 mm, and low spire reaching 27% of total height. Thirteen spiral threads, the shoulder of the sutural ramp bear 13 convex tubercles. The last whorl bears five spiral cords of equal size and five to six narrower ones up to the aperture and over the fasciole (Fig. 4.5–6).

Morphological variant 4

The shell is sub-globose, proportionally less wide than morphological variant 3, with whorls slightly convex in outline. Dimensions are height 44 mm, width 23.6 mm, and spire reaching 32% of total height. Thirteen spiral threads, the shoulder of the sutural ramp bearing 12 slightly pointed tubercles. The last whorl bears six spiral cords of equal size and seven narrower threads up to the aperture and over the fasciole (Fig. 4.7–8).

Morphological variant 5

The shell is sub-globose with whorls squarish in outline. Dimensions are height 32 mm, width 17.7 mm, and relatively high spire reaching 41% of the total height. Thirteen spiral threads, the shoulder of the sutural ramp bears 12 pointed tubercles. The last whorl bears seven spiral cords, the two first ones narrower than the rest, followed by four strong cords of equal size and one narrower cord. There are five narrow threads up to the aperture and over the fasciole (Fig. 4.9).

Morphological variant 6

The shell is sub-globose with slightly convex whorls. Dimensions are height 50.2 mm, width 31 mm, and spire reaching 36% of total height. Twelve spiral threads, the shoulder of the sutural shelf is coronate bearing 13 slightly pointed tubercles. The last whorl bears five strong spiral cords, the first one wider than the rest, followed by at least five narrower spiral threads over the fasciole (Fig. 5.1).

Morphological variant 7

The shell is globose, with whorls slightly convex in outline. Dimensions are height 42.2 mm, width 26.6 mm, and spire reaching 29% of the total height. Twelve spiral threads, the shoulder of the sutural shelf bear 12–13 pointed tubercles. The last whorl bears six spiral cords of equal size and

eight narrower threads up to the aperture and over the fasciole (Fig. 5.2–3).

Morphological variant 8

The small shell is globose, with whorls slightly convex in outline. Dimensions are height 30.4 mm, width 25.5 mm, and low spire reaching 33% of total height. Thirteen spiral threads, the shoulder of the sutural ramp bears 14 nodose tubercles. The last whorl bears eight spiral cords of equal size that are followed by seven to eight narrower cords decreasing in size up to the aperture and over the fasciole (Fig. 5.4).

SYSTEMATIC PALEONTOLOGY

Superfamily STROMBOIDEA Rafinesque, 1815

Family STRUTHIOLARIIDAE Fischer, 1884

Genus *Perissodonta* Martens, 1878

Type species. *Struthiolaria mirabilis* Smith, 1875 by monotypy; Recent, Kerguelen Islands, France.

Remarks. When Steinmann & Wilckens (1908) created *Struthiolarella* to accommodate species previously included in *Struthiolaria* Lamarck, 1816—but characterized differently by transversal sculpture in the older whorls—they included the extant *Struthiolaria mirabilis* Smith, 1875 in *Struthiolarella*. They did not notice, however, that *S. mirabilis* was previously designated the type species of the newly erected genus *Perissodonta* Martens, 1878, thus *Struthiolarella* is now considered invalid and it is a junior synonym of *Perissodonta*. Steinmann & Wilckens (1908) considered, among other characters, the presence of strong cords in the last whorl to differentiated *Struthiolarella* from the apparently uniform strength of the spiral cords in *Perissodonta* (see also Marwick, 1924). However the shell sculpture of both genera shows similar variability in strength of spirals cords on the last whorl surface, as we have observed in extant specimens of *Perissodonta georgiana* Strebel, 1908 (Fig. 6) from Islas Georgias del Sur, housed in the collection of the Museo Argentino de Ciencias Naturales, CABA, Argentina (see also Beu, 2009 and references therein). *P. georgiana* is either

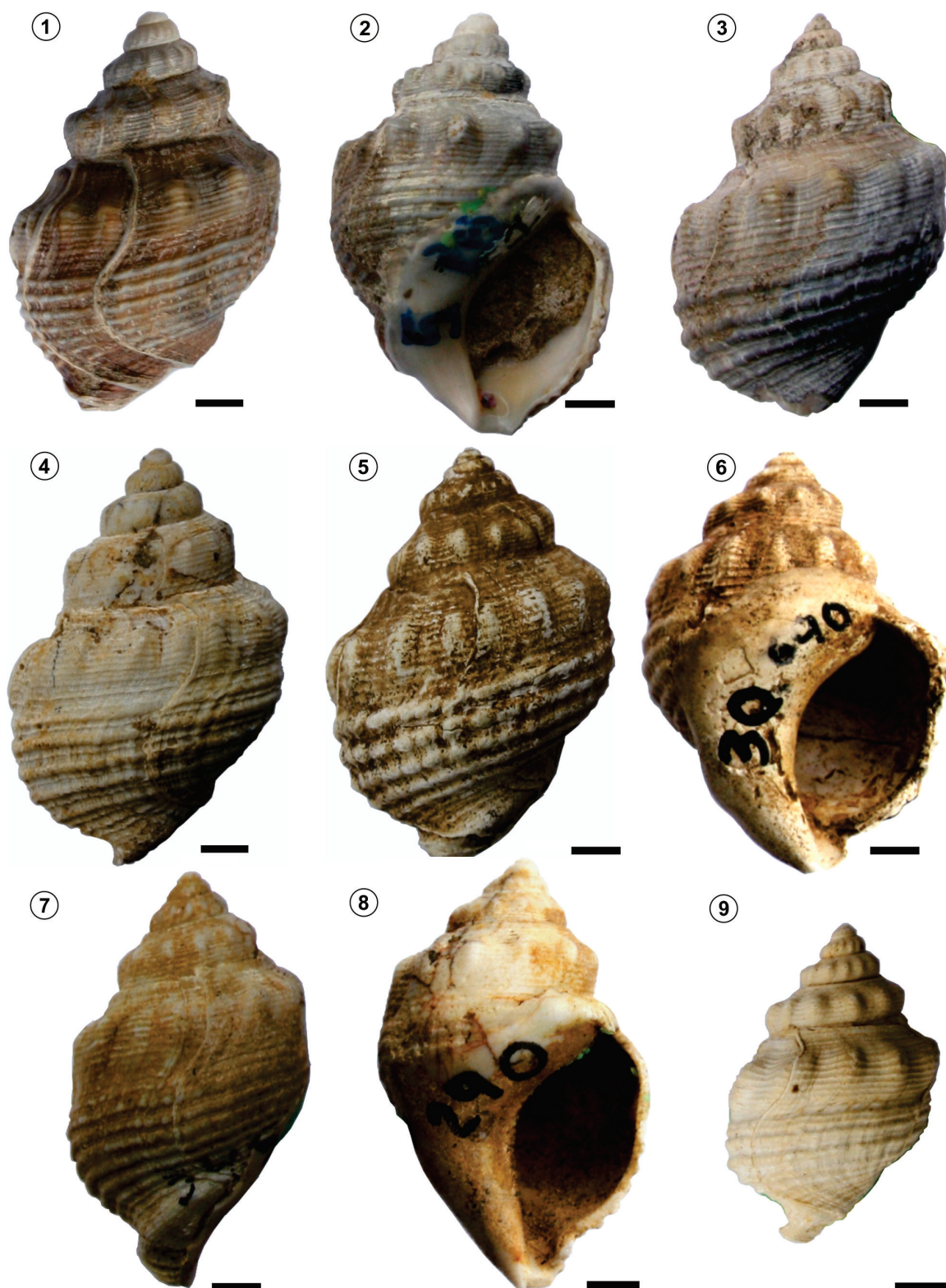


Figure 4. Morphological variability in *P. ameghinoi* from the early Miocene of Tierra del Fuego. 1–2, Morphological variant 1, CADIC PI 612-5, 3, CADIC PI 612-7. Both specimens from Carmen Silva Formation, Punta Basílica beds, Point PB 731. Note marked differences in the spiral cord strength in specimens from the same bed illustrated in 1 and 3. 4, Morphological variant 2, CADIC PI 611-17 Carmen Silva Formation, Carmen Silva beds, Point 545. 5–6, Morphological variant 3, CADIC PI 610-30, Carmen Silva Formation, Carmen Silva beds, Point 690. 7–8, Morphological variant 4, CADIC PI 611-290, Carmen Silva Formation, Carmen Silva beds, Point 545. 9, Morphological variant 5, CADIC PI 611-32, Carmen Silva Formation, Carmen Silva beds, Point 545. Scale bars= 5 mm.

considered a species very close to *P. mirabilis* (Powell, 1951; Morton, 1956), a subspecies of *P. mirabilis* (Strebel, 1908) or even a synonym of it (Troncoso *et al.*, 2001).

In the southern ocean, species of *Perissodonta* are very common in the Eocene of Antarctica; after an apparent gap in the Oligocene they are widespread again in the Miocene of Patagonia and Tierra del Fuego. After the Miocene, the genus is not recorded in Patagonia and Tierra del Fuego and the extant *P. mirabilis* and *P. georgiana* are the only representatives of the family in the southern ocean.

Perissodonta ameghinoi (Ihering, 1897)

Figures 3–5

- 1897 *Struthiolaria ameghinoi* Ihering. Ihering, 1897, p. 289, fig. 14; Ortmann, 1902, p. 201, pl. 33, fig. 11a.
 1908 *Struthiolarella ameghinoi* (Ihering). Steinmann & Wilckens, p. 53, pl. 6, fig. 7.
 1978 *Struthiolarella densestriata* (Ihering, 1897). Malumián *et al.*, p. 282, pl. 2, fig. 2a–b.
 1989 *Struthiolarella fueguina* (Ihering, 1907). Camacho & Zinsmeister, p. 105, pl. 3, fig. 1.
 2005 *Perissodonta ameghinoi* (Ihering, 1897). Nielsen, p. 1126, fig. 4.1–4.3.

Type material. According to Parodiz (1966) there are 12 syntypes under the number 763 in the Ihering collection housed in the MACN-Pi. Monte León Formation, early Miocene. Originally referred to the localities of La Cueva and Río Santa Cruz Mouth (Ihering, 1897), but according to Parodiz (1996) the locality better corresponds to Yegua Quemada, a few miles south of the mouth of the Río Santa Cruz, Santa Cruz Province, Argentina, early Miocene.

Referred Material. Eighty five well-preserved specimens used for measurements, listed in Table 1. From the early Miocene Carmen Silva Formation, Tierra del Fuego: Carmen Silva beds, point 690, 13 specimens (CADIC PI 610); point 545, 52 specimens (CADIC PI 611); point 135, seven specimens (CADIC PI 615); Punta Basílica beds, point PB 731, three specimens (CADIC PI 612); Viamonte Formation, point 164, CADIC PI 616; and Irigoyen Formation, point 841, two specimens (CADIC PI 613). From the early Miocene, Monte León Formation, Mount Entrance, Santa Cruz, six specimens (CADIC PI 617). Several partially preserved specimens from: the Carmen Silva Formation, point 690 CADIC PI 619; point 545 CADIC PI 620; and point PB 731 CADIC PI 621;

the Viamonte Formation, CADIC PI 622; and the Irigoyen Formation, point 841; point 845 CADIC PI 623.

Description. Shell globose to sub-globose, whorls convex to squarish in outline, medium to large size (up to 52 mm in height), height greater than width. Protoconch abraded. Spire shorter than the last whorl (10.1 to 49.5%, usually c. 32–41% of total height). Shell with up to six slightly rounded or squared whorls, with broad, concave sutural ramps and impressed suture. Last whorl with a sub-oval aperture, widening adapically. Columella strongly concave and smooth, with a twisted and narrow fasciole. Inner lip with wide and thick callus, siphonal canal short. Spiral sculpture of four to seven primary basal rounded cords of variable thickness, usually intercalated with second order cords. Surface between adapical cord and suture covered with nine to 13 threads, axial sculpture of 12 to 18 prominent, rounded to pointed, prosocline tubercles that abruptly appear on periphery of sutural ramp.

Remarks. When erecting *Struthiolaria ameghinoi* Ihering (1897) stressed the point of the large size, scalariform outline, elongated nodules, and well-developed spiral cords and threads in this species. These characters were also considered distinctive of *P. ameghinoi* by subsequent authors, including Ortmann (1902), Ihering (1907), Steinmann & Wilckens (1908) and Camacho & Zinsmeister (1989), among others. They are also present in some specimens of Tierra del Fuego. For example, the scalariform (squarish) whorl outline generally mentioned for the Monte León specimens of *P. ameghinoi* (*e.g.*, Fig. 5.6) is recorded in morphological variants 1, 2 and 5 (Fig. 4.1–2, 4.4, 4.9). Conversely, the more convex whorl outline commonly recorded in the Fuegian specimens, *e.g.*, morphological variants 3, 4, 6, 7, and 8 (Fig. 4–5) is also recorded in some of the specimens of *P. ameghinoi* from the Monte Leon Formation (Fig. 5.5). In general, when a large number of specimens are considered in the analysis an intergradation of morphological and sculptural characters, such as relative height of the spire or width of the shell and number of cords, threads and tubercles, is clearly seen in *P. ameghinoi* from Tierra del Fuego and Santa Cruz (Fig. 3.1–3). For these reasons, both "*Struthiolaria*" *fueguina* (see also Camacho & Zinsmeister, 1989) and "*Struthiolarella*" *densestriata*, non Ihering, 1897, described by Malumián *et al.* (1978) for the Carmen Silva Formation are considered in the

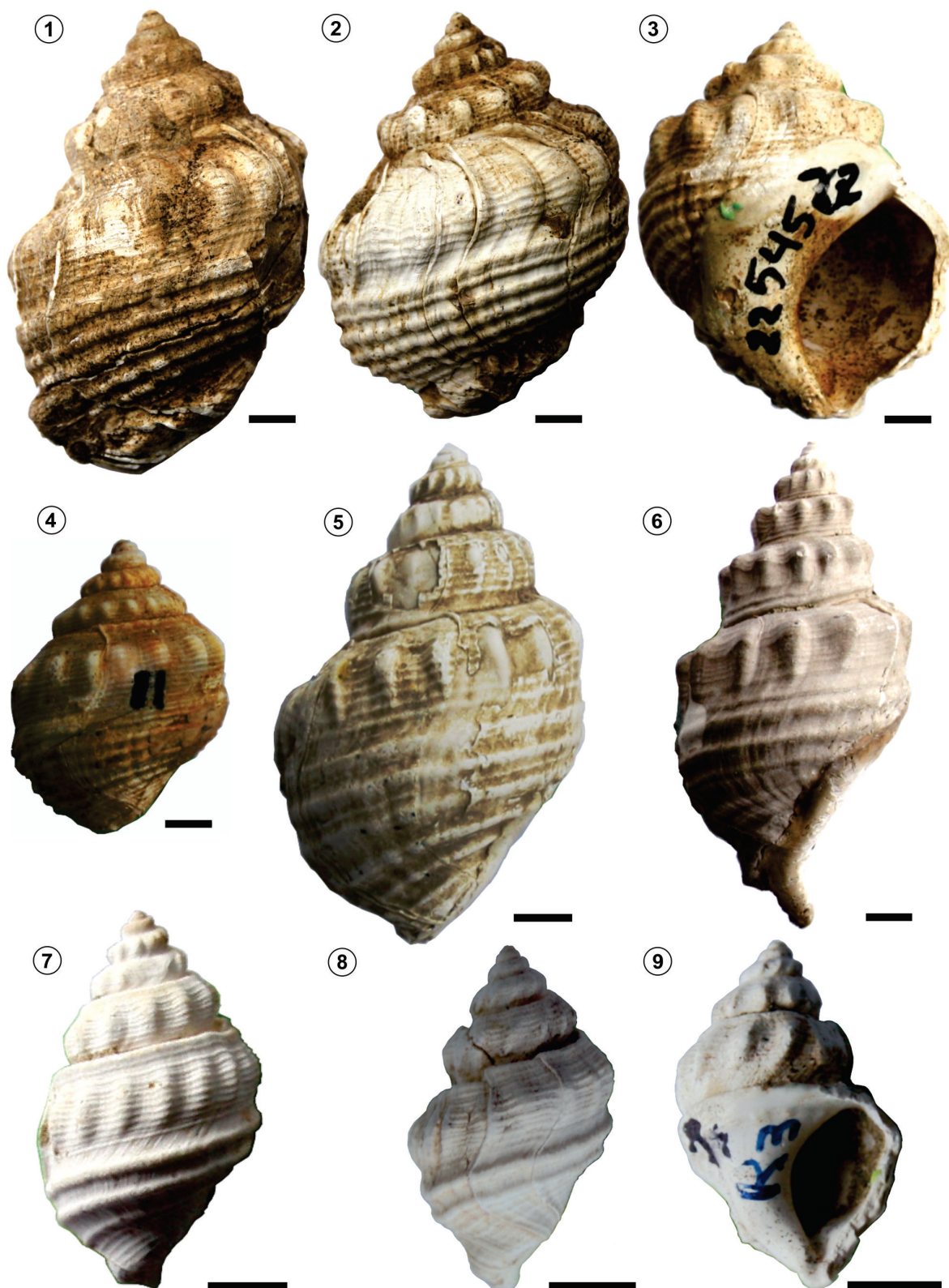


Figure 5. Morphological variability in *P. ameghinoides* from the early Miocene of Tierra del Fuego and Santa Cruz. 1, Morphological variant 6, CADIC PI 610-3, Carmen Silva Formation, Carmen Silva beds, Point 690. 2-3, Morphological variant 7, CADIC PI 611-22, Carmen Silva Formation, Carmen Silva beds, Point 545. 4, Morphological variant 8, CADIC PI 611-11, Carmen Silva Formation, Carmen Silva beds, Point 545. 5-6, *P. ameghinoides* from Mont Entrance, Santa Cruz, E, wide Morphological variant, CADIC PI 617-E21-3; 6, narrow Morphological variant, CADIC PI 617-E21-1. 7-9, *P. ornata* from Piedrabuena, Santa Cruz, G, CADIC PI 618-1; 8-9, CADIC PI 618-2. Scale bars= 5 mm.

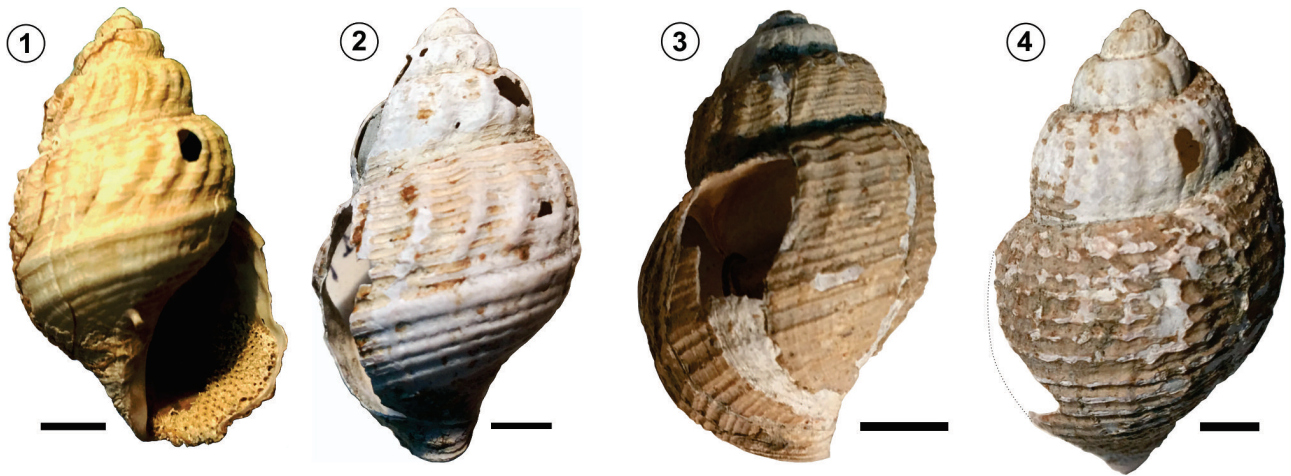


Figure 6. Morphological and ornamental variability in *Perissodonta georgiana* from Islas Georgias del Sur. 1–2, morphological variants with well-differentiated strong spiral cords in the last whorl. Note the variability in the number of tubercles between 1 (high) and 2 (low); 1, MACN-In 36298, Col. Eduardo L. Holmberg; 2, MACN-In 18955. 3, Morphological variant with slight differences in density and strength between spiral cords and threads, MACN-In 18953. 4, Morphological variant with spiral cords of uniform strength, MACN-In 18955 2, 3, 4, Col. Carcelles-Romero. Scale bars= 5 mm

synonymy list of *P. ameghinoi* in the present study.

The struthiolariid gastropods collected in the San Julián Formation at Playa la Mina and Cabo Curioso (Fig. 1) are referred to *Perissodonta* sp., which differs from *P. ameghinoi* in bearing cords and threads of similar strength and a higher number of tubercles, about 18 per whorl.

Geographic and stratigraphic distribution. In Tierra del Fuego *P. ameghinoi* is distributed in the early Miocene Carmen Silva, Viamonte, and Irigoyen formations. *Perissodonta* sp. was also mentioned from the Conglomerado Cerro Águila (Feldmann *et al.*, 2011), which is presently included in the Viamonte Formation (*cf.* Malumián & Olivero, 2006).

Reference to the early Miocene to these formations is not well-constrained but it is supported by calcareous nannoplankton (Bedoya-Agudelo, 2019), foraminifera (Codignotto & Malumián, 1981), molluscan content (del Río, 2021), and petrographic and isotopic data (Torres Carbonell & Olivero, 2019; Olivero & Torres Carbonell, 2021).

DISCUSSION

Previous studies of the Fuegian gastropod genus *Perissodonta* (ex-*Struthiolaria* or *Struthiolarella*) from the Carmen Silva Formation have recognized three species, including *P. ameghinoi*, *P. densestriata*, and *P. fueguina* (Steinmann & Wilckens, 1908; Malumián *et al.*, 1978;

Camacho & Zinsmeister, 1989), but they were based on scarce material. The present systematic study of more than 100 specimens of the gastropod genus *Perissodonta* from different early Miocene stratigraphic units in Tierra del Fuego suggests, on the contrary, that they can be accommodated in a single, plastic species. Specimens of *Perissodonta* in our collection are characterized by highly variable morphological characters, particularly regarding the shell shape and the number and strength of spiral cords, spiral threads, and tubercles. The measurements of different shell shape attributes and counts of ornamental characters demonstrate this continuous variability (Fig. 3). In the plot of the relative height of the spire versus the shell relative width both the material from Tierra del Fuego and topotype specimens of *P. ameghinoi* from Mount Entrance, Santa Cruz cover the same morphospace (Fig. 3.1), forming a continuous trend, with no distinct cluster of points. Similarly, the plot of the shell height and width shows a continuous trend and intergradation among shell-shape parameters (Fig. 3.2). Accordingly, following the original suggestion of Steinmann & Wilckens (1908) we have included in *P. ameghinoi* all the Tierra del Fuego material previously assigned to *P. densestriata* and *P. fueguina* (Malumián *et al.*, 1978; Camacho & Zinsmeister, 1989).

Nonetheless, there are some slight differences in the shell shape of some specimens, which may be attributed to

geographic variations. According to the interpretation of *P. ameghinoi* given by Ihering (1897) and Ortmann (1902) the scalariform (squarish) whorl outline (e.g., Fig. 5.6) seems to be more common in the area of provenance of the type material in Santa Cruz. However, specimens with both convex and scalariform outlines coexist in the same bed in the Santa Cruz and Fuegian material but seemingly with different frequencies, being the convex whorl morphs more common in Tierra del Fuego and vice versa, supporting the idea of geographic variants of a single species.

Among the species of *Perissodonta* described from the early Miocene of Santa Cruz and Tierra del Fuego the oldest available names are *P. ornata* and *P. ameghinoi* (cf. Ihering, 1897; Steinmann & Wilckens, 1908; Griffin & Nielsen, 2008). *P. ornata* is clearly a very distinctive species (Fig. 5.7–9), which according to its canaliculated suture and the two or three strong cords in the last whorl can be readily distinguished from *P. ameghinoi* (cf. Marwick, 1924). This distinction is evident since both the shell shape parameters and number of ornamental characters form distinctive clusters, occupying a different morphospace than in *P. ameghinoi* (Fig. 3.2).

The interpretation of the rest of the *Perissodonta* species from other Eocene (Río Turbio Formation; Loreto Formation; La Meseta Formation), Oligocene (San Julián Formation), and early Miocene (Centinela–25 de Mayo and Chacay formations) deposits from Antarctica, Santa Cruz and Chile (see Zinsmeister & Camacho, 1980; Camacho & Zinsmeister, 1989; del Río, 2002), is beyond the scope of this study. Nonetheless, direct comparison with available material from these formations, indicates that the Eocene material is quite different from the Miocene *P. ameghinoi*. *Perissodonta hatcheri* from the Eocene Loreto Formation, Punta Arenas, Chile, and *P. variabilis* (Wilckens, 1911) and *P. shackletoni* (Zinsmeister & Camacho, 1980), from the Eocene La Meseta Formation, Seymour Island, Antarctica (cf. Zinsmeister & Camacho, 1980; Camacho & Zinsmeister, 1989), have spiral cords of equal size and strength all over the shell, differing from the rest of the species of *Perissodonta*.

The latest Oligocene–earliest Miocene *Perissodonta* sp. from the San Julián Formation is characterized by the slight difference in strength of spiral cords and threads, and by the high number of tubercles, and thus it differs from the early

Miocene *P. ameghinoi*. Moreover, *Perissodonta* sp. was the only struthiolariid observed by the present authors in the San Julián Formation. We were unable to reproduce the finding of the material figured by Camacho & Zinsmeister (1989) and described under *P. ornata*. Incidentally, this material (Camacho & Zinsmeister, 1989: pl. II, fig. 3), however, lacks the characteristic canaliculated suture of *P. ornata* and bear six strong cords in the last whorl; hence it is quite different from Sowerby's species (see also Griffin & Nielsen, 2008).

CONCLUSIONS

In the study of the fossil material of the struthiolariid gastropod *Perissodonta* from Tierra del Fuego we have reached the following conclusions.

1) *Perissodonta* is abundantly distributed in several early Miocene formations in Tierra del Fuego, including the Carmen Silva, Viamonte, and Irigoyen formations.

2) The number, strength, and density of spiral cords, spiral threads, and tubercles are highly variable in the studied material. Furthermore, the plot of morphological and ornamental parameters covers a continuous morphospace in the Fuegian material, thus it is not possible to use these characters for species differentiation.

3) The range of variability in the morphological and ornamental parameters in the Fuegian material is similar to that of *Perissodonta ameghinoi* from its type locality in early Miocene, Monte León Formation, Santa Cruz Province and, following the original suggestion of Steinmann & Wilckens (1908), we assigned the Fuegian material to the same species.

4) The plot of similar morphological and ornamental parameters in *Perissodonta ornata*, also from the Monte León Formation, shows a distinct cluster, covering a different morphospace that clearly distinguishes this species from *P. ameghinoi*.

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